Differential Selection of Crab *Chionoecetes opilio* and *Hyas* spp. as Prey by Sympatric Cod *Gadus morhua* and thorny skate *Raja radiata*

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Abstract. – During 1981 and 1982, 933 Atlantic cod *Gadus morhua* and 119 thorny skate *Raja radiata* were collected off the northwestern coast of Cape Breton Island, Nova Scotia. Danish seines, jigs, gillnets, and trawls were used for sampling. Stomach contents were analyzed to investigate predator-prey relationships between cod and snow crab *Chionoecetes opilio*, two commercially important species. For comparison, skate and two toad crab species, *Hyas araneus* and *H. coarctatus*, were also considered.

During spring (April, May), cod fed mostly (by weight) on large soft-shelled male snow crab [77–110 mm carapace width (CW)]. In summer (July) and fall (September), cod predation was directed more towards prey species such as fish, although the mean number of snow crab per cod stomach also increased. The average number of snow crab in cod stomach contents was higher (0.59 crab/stomach) on sand and mud bottoms than on rocky and gravel bottoms (0.05 crab/stomach). In contrast, higher numbers of toad crab (1.35 crabs/stomach) were found in stomachs from cod on rocky and gravel bottom than on mud and sand bottom (0.50 crab/stomach).

There were approximately five times more snow crab (by number) in the stomachs of skate than in cod. The frequency of toad crab present in the stomach contents of both predators was similar. On average, individual skate consumed up to five times more snow crab (by number) than toad crab, while cod consumed approximately equal numbers of toad and snow crab. Estimates of crab abundance provide evidence that cod feed more on toad crab than snow crab, whereas skate seem more opportunistic.

Problems associated with using stomach content analysis to assess the potential impact of cod predation on snow crab recruitment are discussed.

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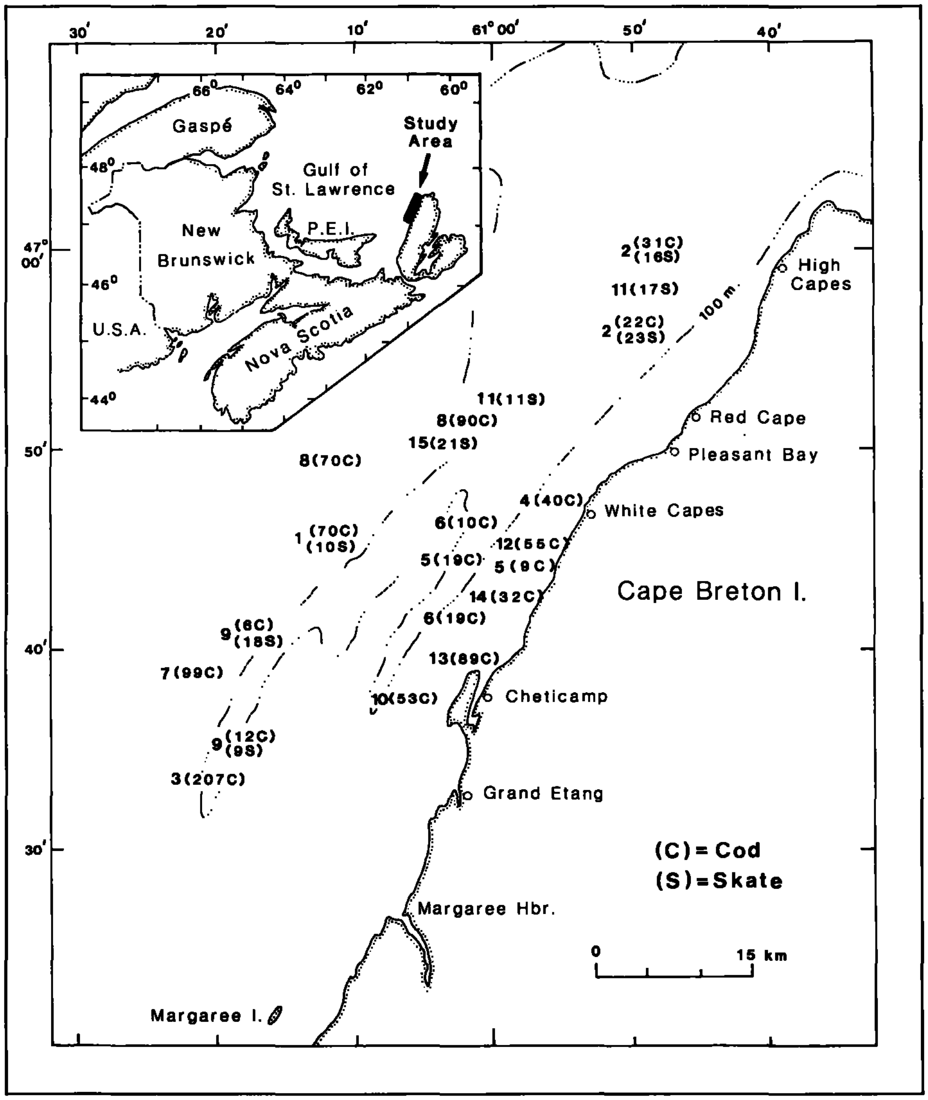
Cod *Gadus morhua* and snow crab *Chionoecetes opilio* which in 1983 supported fisheries valued at $17.4 and $29.1 million, respectively, form two of the most important fisheries in the Gulf of St. Lawrence (Anon. 1982; Elner and Bailey 1986). The snow crab resource is heavily exploited, and the fishery has become almost entirely dependent on the recruitment of crab reaching commercial size each year (Bailey and Elner 1989). Little is known about the factors affecting snow crab recruitment. Past studies on the east coast of Canada have established a predator:prey linkage between cod and snow crab (Waiwood et al. 1980, Waiwood 1981, Bailey 1982, Waiwood and Elner 1982, Lilly and Rice 1983, Lilly 1984, Lilly and Botta 1984, Waiwood and Majkowski 1984). Bailey (1982) suggested that cod predation could be a major factor controlling the number of snow crab entering the fishery each year. However, Waiwood and Elner (1982) suggested that cod do not control recruitment of crab into the fishery, but simply react to the availability of crabs as compared with other prey species.

Although cod has been identified as an important predator of snow crab, the ecological mechanisms involved in the interaction are not well understood. By analyzing cod stomach contents, this work provides fresh insights into cod predation on crab in nature. We also discuss the problems associated with using stomach contents analysis as a means of assessing the impact of cod predation on snow crab recruitment, and evaluate the use of stomach contents as a biological tool for sampling snow crab. For comparative purposes, skate *Raja radiata*, a known predator on crab (Templeman 1982), and two additional crab prey species commonly recognized as toad crab (*Hyas araneus* and *H. coarctatus*) were considered in the study.

Materials and methods

Over the period 21 April 1981 to 29 September 1982, 933 cod and 119

Figure 1
Location of study area and sampling sites during 1981–82. Numbers in parentheses indicate the number of fish sampled, and numbers outside parentheses are sample identification numbers. Data from sites with the same sample number were combined for the analysis.



skate stomachs were collected off the northwestern coast of Cape Breton I. (Fig. 1). Sampling was conducted on an opportunistic basis from various fishing vessels and during research cruises; consequently, different gear types were used (Danish seines, jigs, gillnets, trawls) (Robichaud 1985). Data from samples collected at adjacent sites, on similar bottom, during the same week period and using the same sampling gear were combined and assigned the same sample number (Fig. 1).

Fork length of cod and total length of skate were measured at sea. However, in samples 3 and 8 where large numbers of cod were caught (207 and 160 cod, respectively), all stomachs were removed but, due to limited time, only a random subsample of cod was measured. Possible differences in mean sizes of cod and skate between samples were tested by a "one-way" analysis of variance combined with a Duncan test (Duncan 1955) after transforming the data with Log(x).

Stomach removal was performed by (1) tying off the anterior part of the stomach with plastic "spaghetti" tubing identified by a specimen number, and (2) separating the esophagus in front of the tubing and cutting the posterior part of the pylorus in order to prevent the loss of stomach contents. Stomachs were then preserved in 4% formaldehyde and seawater and transported to the laboratory for analysis. For each cod and skate, data on capture location, depth, bottom type, and gear type were recorded.

In the laboratory, stomach contents were examined and prey remains identified to the lowest taxonomic level that the state of digestion permitted. Food in each taxon was weighed and its contribution, in terms of percent by weight of the stomach contents, was determined. All unidentified portions and material such as vegetable matter, stones, and mucous were categorized as "others". Empty stomachs, which accounted for less than 9% of the total stomachs sampled, were not used in the analysis. Crab prey were individually identified to species, weighed, measured [carapace width (CW)] and sexed. For each sample, total number of individuals for each crab species, total weight of individuals, frequency of occurrence, and mean number of crabs per stomach were determined. Size-frequency distributions were constructed for each crab species. Relationship between the carapace width of crab and body length of cod or skate predator was also assessed using scattergram plots.

The bottom substrate was sampled using a Van Veen grab. Substrate characteristics were also based on sediment information, collected also with a Van Veen grab, during a juvenile snow crab survey done concurrently with this study (Robichaud 1985, Robichaud et al. 1989).

Results

The average number of *H. araneus* and *H. coarctatus* per cod stomach was 0.37 [variance (S) 1.04] and 0.42 (S 1.82), respectively. Predation by cod on the two toad crab species followed similar patterns. The average number of both toad crab species per cod stomach was higher on gravel bottom [0.59 (S 1.54) and 0.53 (S 1.69) for *H. araneus* and *H. coarctatus*, respectively] and lower on sand and mud bottom [0.19 (S 0.56) and 0.33 (S 1.93) for *H. araneus* and *H. coarctatus*, respectively]. In addition, the number of both toad crab species per skate stomach was low [0.02 (S 0.02) and 0.06 (S 0.16) for *H. araneus* and *H. coarctatus*, respectively]. Because there was no significant differences ($P>0.05$, using t-test) in number per stomach between the two toad crab species, and because of the large proportion (23%) of toad crabs that was unidentifiable and categorized as *Hyas* species, all toad crabs were combined for the stomach analysis.

There were significant differences ($P<0.05$) in the average size of cod between samples (Fig. 2). There were no significant differences ($P>0.05$) in the mean size of skate between samples (Fig. 2).

Cod stomach analyses

The stomach contents of cod caught by Danish seiners or by trawls over deep (100–141 m) muddy or sandy bottoms during the spring of 1981 and 1982 comprised a large percentage by weight of snow crab (Fig. 3; Table 1, samples 1–3). The percentage by weight of snow crab found in cod stomachs ranged between 40.4

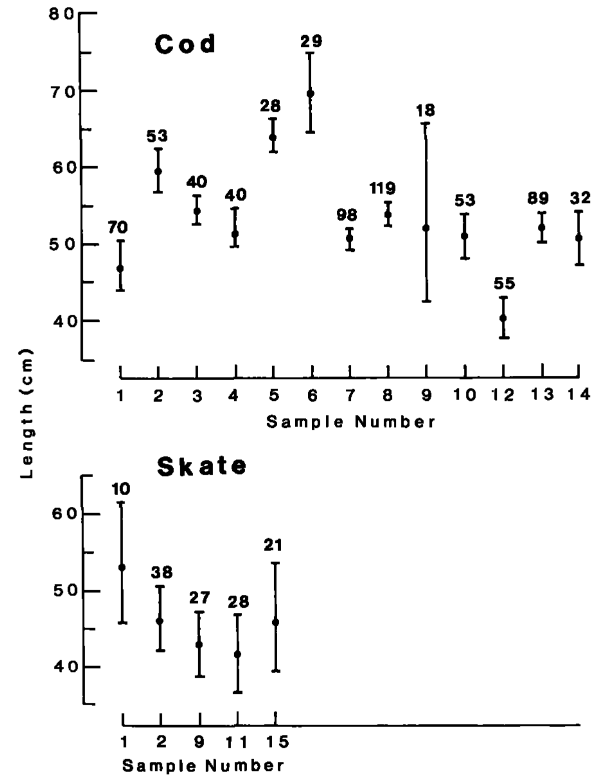


Figure 2

Geometrical mean size of cod and skate for each sample collected during 1981–82. Dots are means; vertical lines are ±95% confidence limits; numbers above dots are the number of fish in each sample.

and 66.2%. The mean number of snow crab per cod stomach ranged between 0.13 and 0.39, respectively (Fig. 3; Table 1). In the same samples, the percentage by weight of toad crab (*Hyas araneus* AND *H. coarctatus*, combined) ranged between 1.8 and 5.2%, and the mean number of toad crab per cod stomach ranged between 0.10 and 0.53 (Fig. 3; Table 1). The high percentage of the total weight of snow crab in cod stomachs during spring was mainly made up of large soft-shelled males. Whole soft-shelled crabs were usually found compacted into a single pliable ball in cod and skate stomachs. On removal from the stomachs, they could be unfolded and measured. Other prey taxa identified were invertebrates, such as amphipods, euphausiids, and molluscs, and minor quantities of fish (Fig. 3, samples 1–3).

In May 1982, cod taken by jigging over gravel bottom at shallow depth (55 m) contained a negligible amount of snow crab (0.4% of overall weight) (Fig. 3, sample 4). In the same sample, the percentage by weight of toad crab was higher (27.8%) and the mean

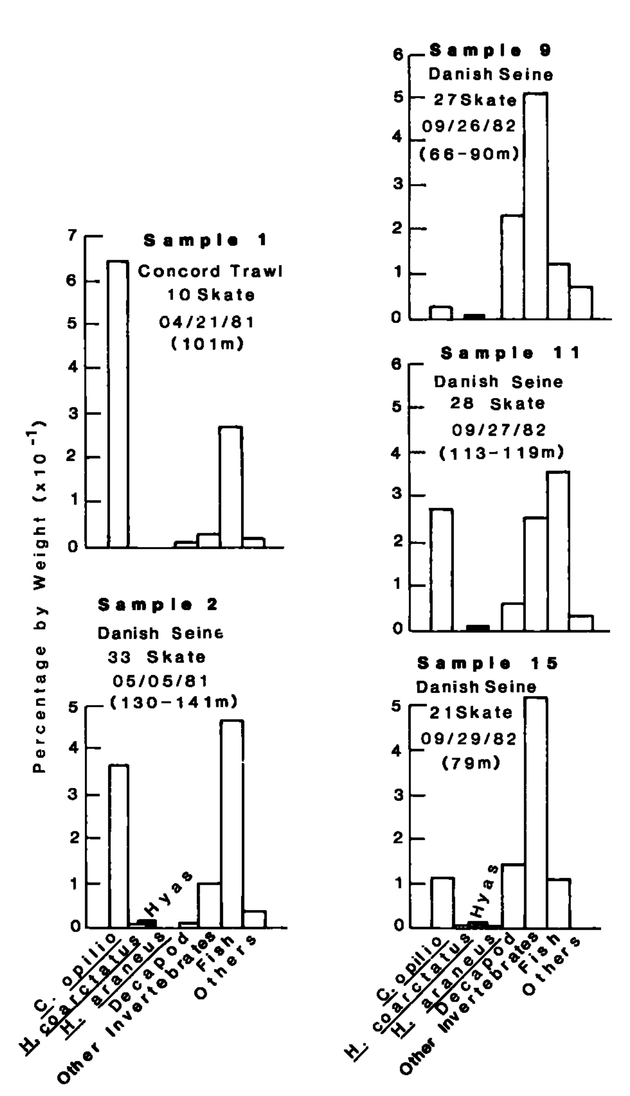


Figure 3
Percentage by weight of prey categories against total weight of stomach contents from cod sampled in April/May 1981 and May 1982. Dark bar represents the percentage by weight of toad crabs (*Hyas araneus*, *H. coarctatus*, unidentified *Hyas*); depth range given in meters.

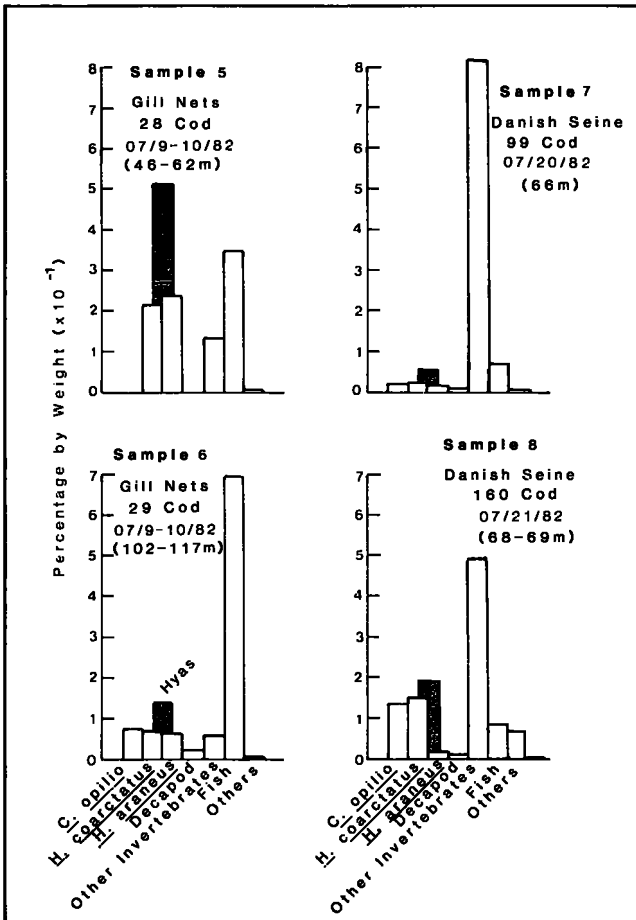


Figure 4
Percentage by weight of prey categories against total weight of stomach contents from cod sampled in July 1982. Dark bar represents the percentage by weight of total toad crabs (*Hyas araneus*, *H. coarctatus*, unidentified *Hyas*).

number of toad crab per stomach was 1.63, compared with 0.05 for snow crab (Fig. 3; Table 1). In this sample, there was also a large proportion (39.9%) of other invertebrates consumed.

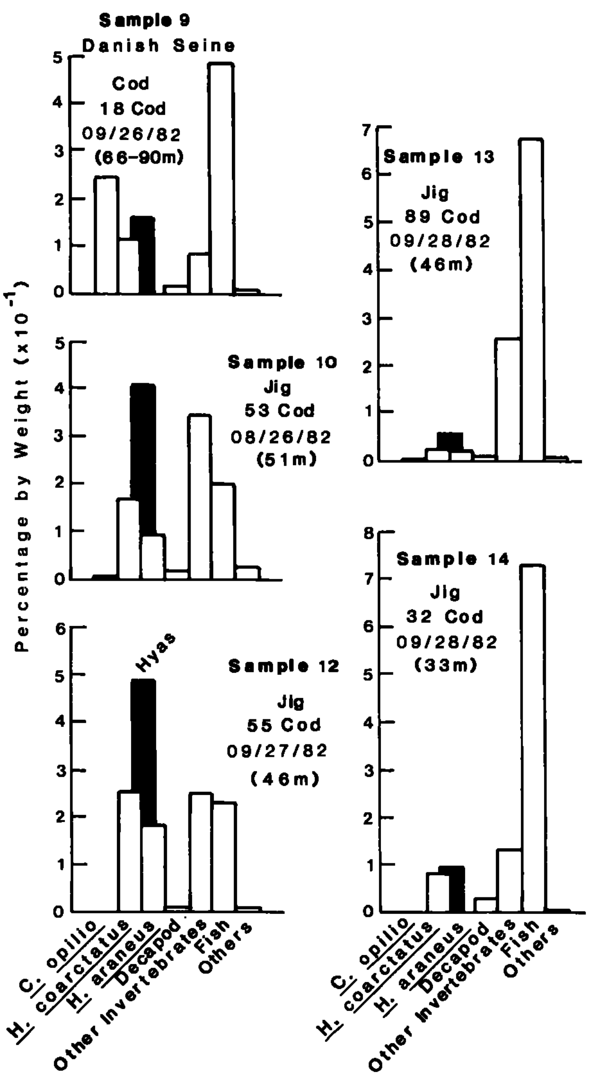
During July 1982, in cod sample 5, taken with gillnets set on gravel bottom in shallow water (46–62 m), there were no snow crab (Fig. 4). However, the percentage by weight of toad crab was 51.2%, and the average number of toad crab per cod stomach was 2.0. For sample 6, from the stomach contents of cod also captured by gillnets, but in deeper water (102–117 m) on mud bottom mixed with boulders, the percentage by weight of snow crab was 7.4% and the mean number of snow crab per cod stomach was 0.17 (Fig. 4; Table 1). In comparison with sample 5, the percentage by weight of toad crab in sample 6 decreased to 14.7% and the mean number of toad crab per cod stomach was 1.65 (Fig. 4; Table 1). In cod samples 5 and 6, the major diet percentages of total weight were fish (34.7 and 69.6%, respectively) such as pleuronectids and gadids (Fig. 4).

In July 1982, for stomachs of cod taken by Danish seiners over shallow (66–69 m) sandy and muddy bottoms (Fig. 4, samples 7 and 8), the percentage by weight of snow crab was 2.2 and 13.8%, respectively. This percentage of total weight was lower than that found in cod stomachs taken on similar but deeper (101–141 m) bottoms during spring 1981 and 1982 (Fig. 3, samples 1–3). However, the mean number of snow

Table 1
Snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* occurring in cod stomachs (with food).

Sample no.	Depth (m)	Date (MDY)	Stomachs sampled	Percentage by weight: Snow crab	Percentage by weight: Toad crab	Frequency of occurrence: Snow crab	Frequency of occurrence: Toad crab	Mean number per stomach: Snow crab	Mean number per stomach: Toad crab
1	101	04-21-81	70	40.4	5.2	8.6	4.3	0.13	0.10
2	130–141	05-05-81	53	59.2	4.5	26.4	13.2	0.38	0.53
3	101	05-10-82	207	66.2	1.8	33.3	8.7	0.39	0.19
4	55	05-28-82	40	0.4	29.8	2.5	36.9	0.05	1.63
5	46-62	07-9/10-82	28	—	51.2	—	53.6	—	2.00
6	102–117	07-9/10-82	29	7.4	14.7	10.3	48.3	0.17	1.65
7	66	07-20-82	99	2.2	5.7	30.3	18.2	0.47	0.37
8	69	07-21-82	160	13.8	18.1	52.5	42.5	1.16	1.16
9	66–90	09-26-82	18	24.5	16.1	27.8	16.7	0.78	0.22
10	51	09-26-82	53	0.1	40.8	7.5	52.8	0.08	1.57
12	46	09-27-82	55	—	48.8	—	49.1	—	1.96
13	46	09-28-82	89	0.1	5.5	1.1	27.8	0.01	0.49
14	33	09-28-82	32	—	9.7	—	25.0	—	0.78

Figure 5
Percentage by weight of prey categories against total weight of stomach contents from cod sampled in September 1982. Dark bar represents the percentage by weight of total toad crabs (*Hyas araneus*, *H. coarctatus*, unidentified *Hyas*).



crab per cod stomach for samples 7 and 8 had increased to 0.47 and 1.16, respectively (Table 1). The percentage by weight of toad crab in cod samples 7 and 8 was 5.7 and 18.1%, respectively. The mean number of toad crab per cod stomach (0.37 and 1.16 crab/stomach, respectively) was similar to the mean number of snow crab found in the same cod stomach samples (0.47 and 1.16 crab/stomach, respectively) (Fig. 4; Table 1). In samples 7 and 8, cod had concentrated their feeding on other invertebrates (49.7 and 82%, respectively) such as euphausiids, gastropods and polychaetes.

During September 1982, in cod sample 9, taken by Danish seiners on muddy or sandy bottom at intermediate depths (66–90 m), the percentage by weight of snow crab was 24.5%, and the mean number of snow crab per stomach was 0.78 (Fig. 5; Table 1). The increase in the percentage by weight of snow crab in September is a consequence of a size increase of juvenile crab ingested in September (13.2 g/crab) compared with July (3.7 g/crab). The percentage by weight of toad crab in sample 9 was 16.1%, and the average number of toad crab per cod stomach was 0.22 (Fig. 5; Table 1). The largest percentage of total weight in sample 9 was composed of fish (48.6%) such as mackerel *Scomber scombrus*, pleuronectids, and smaller gadids.

Cod captured with jigs at sites a few kilometers from shore on shallow (46–51 m) gravel bottom (samples 10 and 12) consumed negligible amounts of snow crab (Fig. 5; Table 1). In contrast, the percentage by weight of toad crab in samples 10 and 12 was 40.8 and 48.8%, respectively, and the mean number of toad crab per cod stomach was 1.57 and 1.96, respectively (Fig. 5; Table 1). Other important prey in the diet of these cod were invertebrates (25.4 and 34.7%) (amphipods, euphausiids, and molluscs) and fish (20.2 and 23.3%) [pleuronectids, mackerel *Scomber scombrus*, and small gadids].

Cod captured with jigs at sites closer to shore on shallower (33–46 m) gravel bottom (samples 13 and 14) also consumed negligible amounts of snow crab (Fig. 5; Table 1). However, the percentage by weight of toad crab was lower, 5.5 and 9.7%, as was the mean number per stomach, 0.49 and 0.78 (Fig. 5; Table 1). In addition, stomachs contained *Cancer* crab and a lobster *Homarus americanus*, but the main prey once again was fish (67.7 and 73.2%) (Fig. 5).

Skate stomach analyses

All skate were collected during spring 1981 and fall 1982 by Danish seines or concord trawls over sandy and muddy bottoms (Fig. 1) (samples 1, 2, 9, 11, and 15). During spring 1981 (samples 1 and 2), the percentage by weight of snow crab found in skate stomachs was 37.7 and 64.3%, and the mean number of snow crab per stomach was 0.30 and 2.26 (Fig. 6; Table 2). The large percentage by weight of snow crab present was large soft-shelled males. Besides crab, skate fed on fish (27.4 and 46.9%) such as cod, hake *Urophysis tenuis*, herring *Clupea harengus*, and sand lance *Ammodytes americanus*.

During September 1982 (samples 9, 11, and 15), the percentage by weight of snow crab had decreased to between 3.5 and 27.6%, but the mean number of snow crab per skate stomach had increased to between 1.44 and 4.81 (Fig. 6; Table 2). The overall average number of crab per stomach was twice as high during the fall as in spring. During fall 1982, skate diet also included large quantities of other invertebrates (up to 52%) (polychaetes, amphipods, euphausiids, gastropods, cephalopods, hermit crab *Pagurus longicarpus*, and brittle stars *Ophiopholis aculeata*) and fish (up to 35%) (Fig. 6) such as mackerel *Scomber scombrus* and pleuronectids.

Comparisons between cod and skate as crab predators

The percentage by weight of toad crab in the diet of skate was small (0–1.3%) (Fig. 6; Table 2). However,

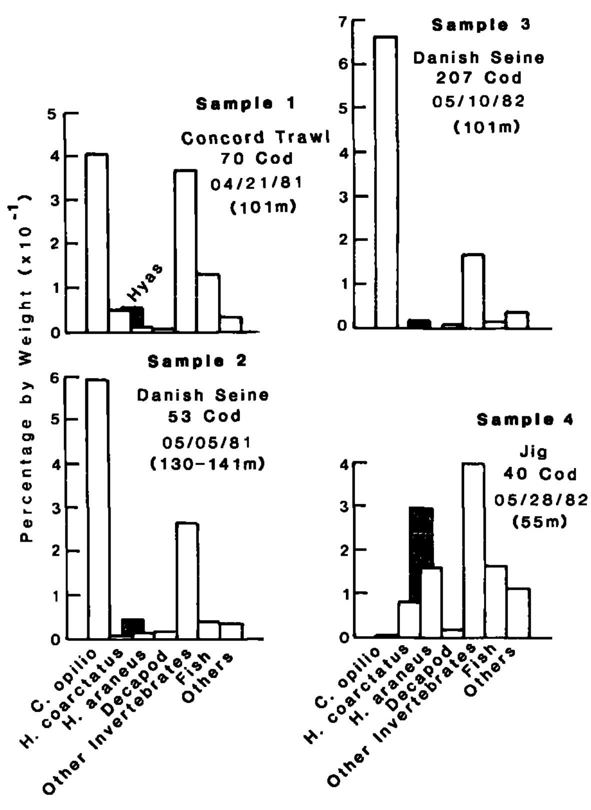


Figure 6
Percentage by weight of prey categories against total weight of stomach contents from skate sampled in April/May 1981 and September 1982. Dark bar represents the percentage by weight of total toad crabs (*Hyas araneus, H. coarctatus*, unidentified *Hyas*).

the mean numbers of toad crab per stomach for cod and skate captured at the same sampling sites in the same tows were similar (0.28 and 0.30 for cod and skate, respectively) (Table 3, samples 1, 2, and 9). In these same samples, the mean number of snow crab found in skate stomachs was on average 4.9 times higher than the mean number of toad crab (Table 3), whereas the mean numbers of snow crab and toad crab found in cod stomachs were similar (0.30 and 0.28, respectively). Skate also appeared to consume up to five times more snow crab than cod (1.60 and 0.30 per skate and cod, respectively) (Table 3).

Influence of season and substratum type

The quantity of crab consumed by cod varied between bottom types. In the stomachs of cod captured on sand and mud bottoms, the overall mean numbers of snow crab and toad crab per stomach were generally similar

Table 2

Snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* occurring in skate stomachs (with food).

Sample no.	Depth (m)	Date (MDY)	Stomachs sampled	Percentage by weight		Frequency of occurrence		Mean number per stomach	
				Snow crab	Toad crab	Snow crab	Toad crab	Snow crab	Toad crab
1	101	04-21-81	10	64.3	—	40.0	—	0.30	—
2	130–141	05-05-81	33	37.7	0.7	75.8	30.3	2.12	0.58
9	66–90	09-26-82	27	3.5	0.2	51.9	14.8	1.44	0.15
11	113–119	09-27-82	28	27.6	0.05	85.7	3.6	4.64	0.04
15	79	09-29-82	21	11.8	0.01	100.0	4.8	4.81	0.05

Table 3

Mean numbers of snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* per cod and skate stomach for fish captured in the same tows.

Sample no.	Cod			Skate		
	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)
1	70	0.13 (0.26)	0.10 (0.29)	10	0.30 (0.45)	—
2	53	0.38 (0.90)	0.53 (3.65)	33	2.12 (5.81)	0.58 (1.12)
9	18	0.78 (3.13)	0.22 (0.30)	27	1.44 (4.04)	0.15 (0.13)
Total	141	0.30 (0.88)	0.28 (1.56)	70	1.60 (4.67)	0.33 (0.62)

Table 4

Mean numbers of snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* per cod stomach for fish captured by bottom type and seasons.

Season	Sand and mud bottom			Gravel, rocky bottom		
	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)
Spring	330	0.35 (0.52)	0.23 (1.12)	40	0.05 (0.12)	1.63 (6.76)
Summer	259	0.90 (1.82)	0.86 (6.97)	57	0.09 (0.18)	1.82 (7.43)
Fall	18	0.78 (3.13)	0.22 (0.30)	229	0.02 (0.02)	1.14 (5.26)
Total	607	0.59 (1.21)	0.50 (3.69)	326	0.04 (0.06)	1.35 (5.86)

except in the fall. However, the fall sample was small (Table 4). On rocky and gravel bottoms, toad crabs were much more abundant (Table 4). Furthermore, the overall mean numbers of snow crab per stomach from cod captured on mud and sand bottoms were substantially greater than for cod captured on gravel and rocky bottoms. For toad crab, mean numbers per stomach were higher in cod captured on rocky and gravel bottom than from sand and mud bottoms.

Crab:cod size relationship

Three distinct size groups of snow crab were detected (Fig. 7). One group, found only during the spring sampling, was comprised mainly of recently molted males ranging in size between 77 and 107 mm CW (Fig. 7). These soft-shelled crabs were consumed by cod ranging in size between 49 and 66 cm (Fig. 7). The second group of snow crab comprised hard-shelled adult females with eggs. This group of crabs was consumed only by larger cod ranging in size between 67 and 106 cm (Fig. 7). The third and most numerous group of snow crab found in cod was made up of juveniles (of both sexes) ranging between 6 and 44 mm CW. These smaller crabs were found in stomachs of cod ranging between 33 and 82 cm. The size range of juvenile crab consumed by cod appeared to broaden with cod size (Fig. 7). However, the pattern seems to reach a plateau for juvenile crab above 44 mm CW; larger juveniles were not found even in large cod. Larger crab or alternate prey species were present in the stomach contents of cod above 82 cm.

The relationship between the size range of the two *Hyas* species and cod length was similar to the relationship found between snow crab and cod (Fig. 8). The size range of toad crab consumed became broader as cod size increased. However, no toad crab over 46 mm CW were found.

Crab:skate size relationships

The relationship between skate length and the size of snow crab consumed appears different from the relationship between snow crab and cod (Fig. 7 and 9). The size range of juvenile snow crab consumed by skate is narrower, with no juveniles larger than 27 mm CW present, compared with 44 mm CW for juvenile crabs found in cod stomachs. Nevertheless, during the spring of 1981, two large soft-shelled male snow crab were found in skate stomachs, indicating that skate were able to feed on larger snow crab (Fig. 9).

The number of toad crab present in skate stomachs was small (Fig. 9). The size range consumed was narrow (5–21 mm CW) and did not change with skate size.

Size-frequency distributions of crab prey

By visual inspection, up to six distinct size-classes, or molt groups, were determined for snow crab found in cod stomachs (Fig. 10). Five of these molt groups could be correlated to molt groups determined by Robichaud et al. (1989) for snow crab caught by beam trawling during the same period in the same area. The corresponding mean sizes for each of the molt groups were 6.8, 13.9, 19.6, 27.1, and 37.3 mm CW. Only two corresponding molt groups (6.8 and 13.9 mm CW) could

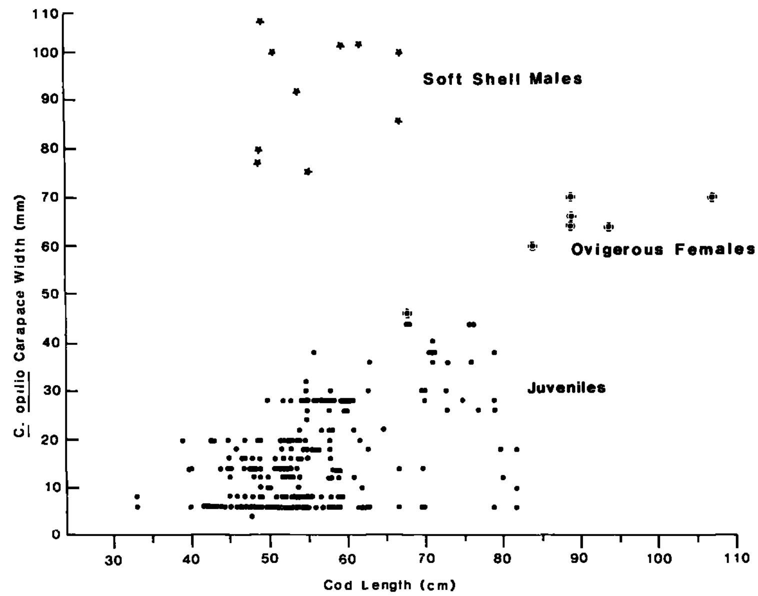


Figure 7
Relationship between carapace width (mm) of *C. opilio* found in the stomachs of cod, and length (cm) of the cod, all cod samples combined for 1981 and 1982.

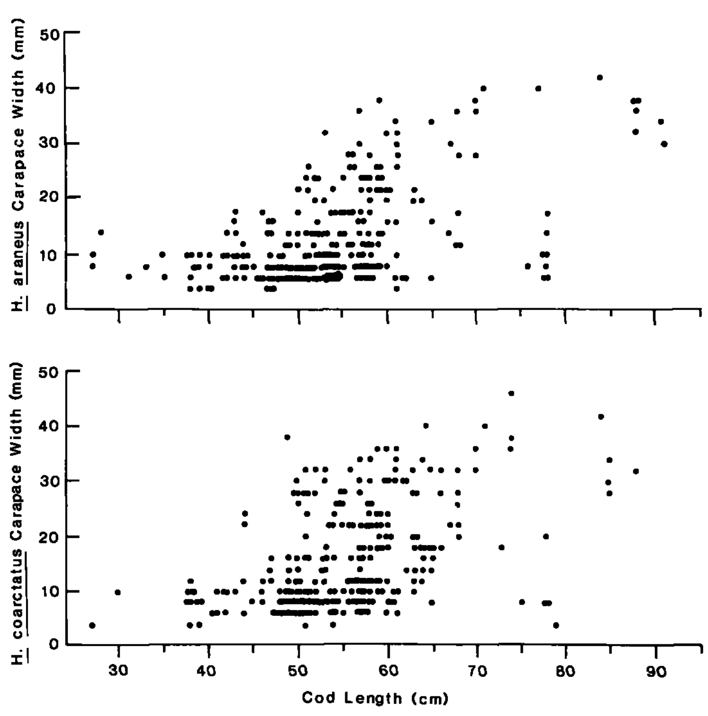


Figure 8
Relationship between the carapace width (mm) of *Hyas araneus* and *H. coarctatus* found in the stomachs of cod, and length (cm) of the cod, all cod samples combined for 1981 and 1982.

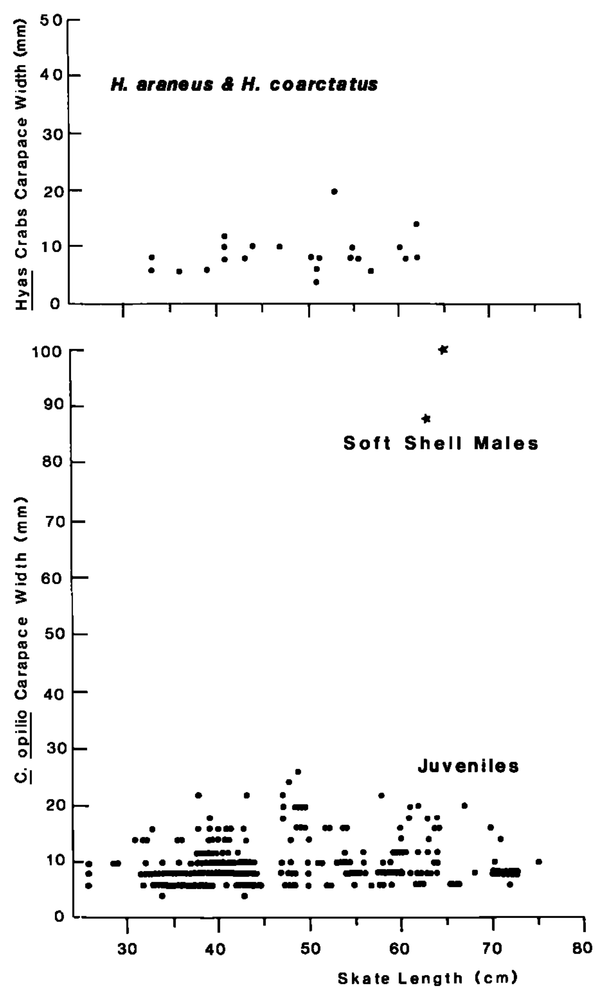


Figure 9
Relationship between the carapace width (mm) of *Hyas araneus*, *H. coarctatus*, and *C. opilio* found in the stomachs of skate sampled in April/May 1981 and September 1982, and the overall length (cm) of the skate.

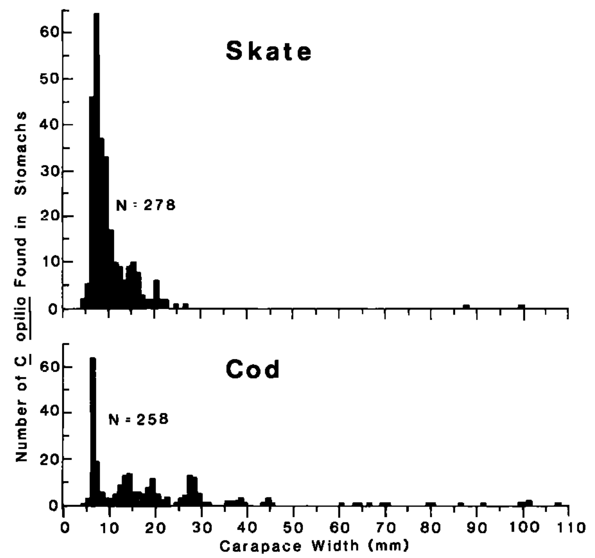


Figure 10
Size-frequency histograms of *C. opilio* found in the stomach contents of all cod and skate sampled in 1981 and 1982.

be identified from snow crab found in skate stomachs (Fig. 10).

The size-frequency distributions of *Hyas araneus* and *H. coarctatus* found in cod stomachs were similar (Fig. 11). However, although molt groups could be determined visually, detailed modal analysis of the distributions was not possible because of the small number of individuals comprising each mode (Macdonald and Pitcher 1979). The maximum size of *Hyas araneus* and *H. coarctatus* found in cod stomachs was 42 and 46 mm CW, respectively.

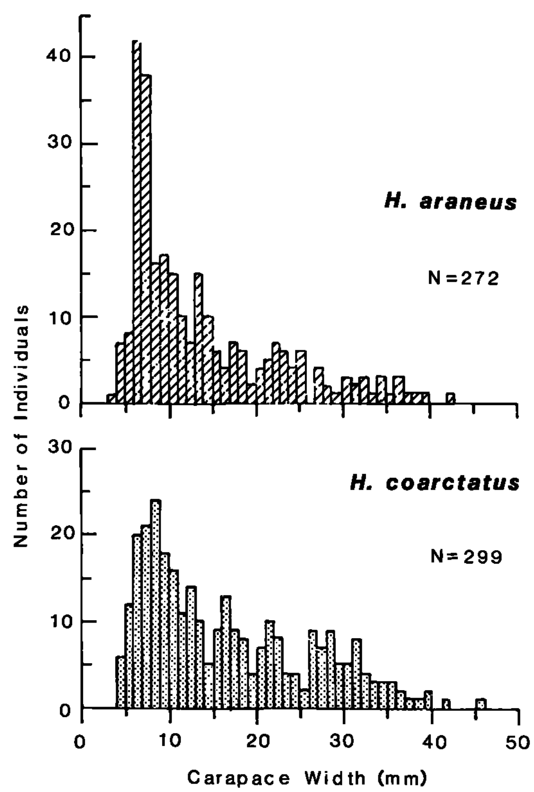


Figure 11
Size-frequency histograms of toad crab found in the stomach contents of all cod sampled in 1981 and 1982.

Discussion

Our study indicates that the diets of cod and skate vary according to season and bottom type. Although there were significant differences ($P<0.05$) in the mean size of cod between some samples which could create some bias in the analyses, the changes in the diet of cod appeared to follow the same general pattern between season and bottom type independent of cod size in each sample (Fig. 2). During spring, cod fed on large soft-shelled male snow crab, while during summer and fall, predation was directed more towards alternate prey species, such as fish and other invertebrates. Seasonal variations in cod diet could reflect the abundance and availability of potential prey species. Such a hypothesis is in accord with Lacroix and Marcotte (1962), Kinnear and Livingstone (1979), Kohler and Fitzgerald (1969), and Corbeil (1954), who argued that seasonal and regional variations in the quantity of prey species eaten by cod are probably due to the distribution of individual prey species, and that prey choice in cod is influenced by prey size, availability, abundance, and ease of capture. Thus, our results may reflect the relative densities and size composition of each crab species present at each sampling site at given times. We found that snow crab were more numerous in cod stomachs from sand and mud bottoms located offshore (0.59 crab/stomach) than on inshore rocky and gravel bottom (0.05 crab/stomach). In contrast, larger numbers of toad crab (1.35 crab/stomach) were found on rocky and gravel bottoms inshore than on mud and sand bottoms offshore (0.50 crab/stomach). We also determined that the two *Hyas* species were present in cod stomachs at similar densities (0.37 *H. araneus* and 0.42 *H. coarctatus*/cod stomach), regardless of bottom type.

Cod and skate appeared to have different feeding patterns for crabs. On average, skate consumed five times more snow crab (1.60 crabs/stomach) than toad crab (0.33 crab/stomach). In contrast, cod captured in the same tows as skate consumed equivalent numbers of snow crab (0.30 crab/stomach) and toad crab (0.28 crab/stomach). Based on a beam trawl survey in the same area during the same periods, Robichaud et al. (1989) determined that snow crab density (11.4 crabs/1000 m^2) was four times higher than the density of toad crabs (2.8 crabs/1000 m^2). If beam trawling is considered to be an unbiased sampling method reflecting the actual densities of both crab species in the area, we can argue that cod feed more on toad crab than snow crab. In contrast, skate would appear to be a more opportunistic predator, feeding on snow crab and toad crab in direct proportion to their actual occurrence.

The stomach contents of cod and skate probably reflect different foraging modes. Cod detect their prey by visual and olfactory cues, but are not capable of detecting buried prey (Brawn 1969). Since snow crab can bury themselves in sediment (Brunel 1960, Miller 1975), cod may experience difficulty in locating them. In comparison, toad crab appear to depend on camouflage rather than burial for protection (D.A. Robichaud, pers. obs.) and are usually found at the sediment surface. As skate prefer foraging in sediment (McEachran et al. 1976), it should be possible for them to detect snow crab buried in mud and sand. In addition, they would also, presumably, be able to locate toad crab on the surface. However, skate may not be as good at catching crabs on the surface.

When attempting to elucidate the impact cod predation could have on snow crab recruitment, many ecological factors need to be considered: distribution patterns of the predator and prey in time and space, size of the predator and prey, availability and vulnerability of the prey, presence of alternative prey species; and behavior of predator and prey. However, one other important non-ecological factor which may influence one's assessment of the relative importance of a prey species in a predator's diet is the method of stomach content analysis employed by the investigator. Different methods of analysis can lead to markedly different conclusions (Hyslop 1980). For example, in this study, if we consider only weight as a measure of the importance of snow crab in cod diet, the greatest quantity of crab present in cod stomachs was during the crab molting period in spring. However, if we consider the actual number of snow crab per stomach or their frequency of occurrence, the number of crab eaten during summer (0.90 crab/stomach) was almost three times higher than spring (0.33 crab/stomach) and the frequency of occurrence was almost twice the spring level (44% vs. 27% in spring). During spring, cod ate fewer but larger soft-shelled male snow crab. During summer and fall, even though the percentage by weight of snow crab was much lower, cod consumed more numerous small juvenile crabs.

Although there are constraints to the present analysis (for example, sampling method, fish size, and the small number of samples), the results provide insight into the predator:prey relationships between fish and crab. However, given the constraints and based on the statistical advice provided, it was decided that any additional effort to statistically isolate the influence of single independent variables such as gear type, season, predator size, depth, or substrate would not only be inappropriate, but liable to create misleading conclusions. For example, studies by Powles (1968), Brêthes et al. (1987), Coulombe et al. (1985), and Robichaud et al. (1989) have shown that substrate is a more important influence than depth on snow crab distribution. We stress that depth, although it may be correlated strongly with crab density, is secondary to substrate type. Studies by Robichaud (1985) and Robichaud et al. (1989) have shown that snow and toad crab densities were not significantly different over a wide depth range for a given substrate and crab species. A study by Scott (1982) on selection of bottom type by 25 species of groundfish, including cod and skate, concluded, even for species like skate which were not strongly associated to bottom type, that depth was not a specific determinant of distribution.

Previous studies on the impact of cod on snow crab recruitment have not taken into account the behavioral and ecological aspects of the two species (Waiwood et al. 1980, Waiwood 1981, Bailey 1982, Waiwood and Elner 1982). The dynamics of benthos:fish trophic interrelationships are complex, and models based on simple expansion of predator abundance and feeding rate data cannot adequately express the "real world" situation.

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