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Submarine canyons as important habitat for cetaceans, with special reference to the Gully: A review

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ABSTRACT

There has been much research interest in the use of submarine canyons by cetaceans, particularly beaked whales (family Ziphiidae), which appear to be especially attracted to canyon habitats in some areas. However, not all submarine canyons are associated with large numbers of cetaceans and the mechanisms through which submarine canyons may attract cetaceans are not clearly understood. This paper reviews some of the cetacean associations with submarine canyons that have been anecdotally described or presented in scientific literature and discusses the physical, oceanographic and biological mechanisms that may lead to enhanced cetacean abundance around these canyons. Particular attention is paid to the Gully, a large submarine canyon and Marine Protected Area off eastern Canada for which there exists some of the strongest evidence available for submarine canyons as important cetacean habitat. Studies demonstrating increased cetacean abundance in the Gully and the processes that are likely to attract cetaceans to this relatively well-studied canyon are discussed. This review provides some limited evidence that cetaceans are more likely to associate with larger canyons; however, further studies are needed to fully understand the relationship between the physical characteristics of canyons and enhanced cetacean abundance. In general, toothed whales (especially beaked whales and sperm whales) appear to exhibit the strongest associations with submarine canyons, occurring in these features throughout the year and likely attracted by concentrating and aggregating processes. By contrast, baleen whales tend to occur in canyons seasonally and are most likely attracted to canyons by enrichment and concentrating processes. Existing evidence thus suggests that at least some submarine canyons are important foraging areas for cetaceans, and should be given special consideration for cetacean conservation and protection.

1. Introduction

Submarine canyons are often described as playing an important role in regional marine ecosystems (Hickey, 1995). There is both anecdotal information and scientific evidence that suggests these distinct topographic features of the continental slope are areas of increased biological productivity and diversity, enhancing all levels of the food chain (Hickey, 1995; Smith et al., 2010). Numerous observations of prey aggregations in submarine canyons have been reported across the globe, including increased abundance of infaunal invertebrates, euphausiids and other crustaceans, and fishes (*e.g.*, Allen et al., 2001; Brodeur, 2001; Cartes et al., 1994; Croll et al., 2005; Greene et al., 1988; Macquart-Moulin and Patriti, 1996; Schoenherr, 1991; Vetter and Dayton, 1998, 1999). Some submarine canyons are even referred to as foraging "hotspots" due to the large number of top-level marine predators such as fish, marine birds and cetaceans that occur within them (*e.g.*, Piatt et al., 2006; Smith et al., 2010; Yen et al., 2004).

There has been much research interest in the use of submarine canyons by some species of cetaceans, such as beaked whales (family Ziphiidae), which appear to be especially attracted to canyon habitats in some areas. For example, the highest sighting rates of northern bottlenose whales (*Hyperoodon ampullatus*) and Sowerby's beaked whales (*Mesoplodon bidens*) off Nova Scotia, Canada, occur within canyon habitats (Hooker et al., 1999; Whitehead, 2013; Wimmer and Whitehead, 2004). Sightings of Cuvier's beaked whales (*Ziphius cavirostris*) are associated with submarine canyons in the Bay of Biscay west of France and in the Gulf of Genoa in the Mediterranean Sea (D'Amico et al., 2003; Moulins et al., 2008; Smith, 2010; Williams et al., 1999). In the Bahamas, Blainville's beaked whales (*Mesoplodon densirostris*) are most commonly sighted within canyon habitats (Claridge and Durban, 2008; MacLeod and Zurr, 2005). Sighting rates of beaked whales during vessel-based surveys off the northeast coast of the United States between 1990 and 1998 were significantly higher in

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canyon regions as compared to non-canyon shelf-edge regions (Waring et al., 2001). However, sightings of northern bottlenose whales in the Davis Strait and off Newfoundland and Labrador, Canada, and sightings of Cuvier's and other unidentified beaked whales in the eastern tropical Pacific, do not appear to be associated with submarine canyons (COSEWIC, 2011; Ferguson et al., 2006; Wade and Gerrodette, 1993). The importance of submarine canyon habitats to beaked whales, (and to cetaceans in general), is thus not entirely clear. Furthermore, the processes by which submarine canyons may attract cetaceans are generally not well understood.

The purpose of this review is to summarize reports of cetacean associations with submarine canyons and investigate the physical, oceanographic and biological processes that may lead to enhanced cetacean abundance and density around these features. The following sections provide an overview of available evidence for increased cetacean abundance within specific submarine canyons and examine trends in the physical characteristics of these canyons and the species that tend to be associated with them. Following on from this, the typical circulation patterns and processes that occur in submarine canyons which may lead to enhanced cetacean prey density are discussed. As a case study, cetacean associations with the Gully (a submarine canyon located off eastern Canada especially well known for high cetacean diversity and abundance) and the mechanisms likely to result in increased prey density within this canyon, are described in greater detail. The final section of this review provides a summary of my main findings and identifies knowledge gaps that should be addressed to gain a more complete understanding of the importance of submarine canyons to cetaceans.

2. Cetacean associations with submarine canyons

In this section, a summary of some cetacean associations with submarine canyons that have been anecdotally described or documented in scientific literature is provided. It is important to note that while studies on cetacean distribution and abundance within and around submarine canyons exist, the amount of data available is limited and biased towards a few well-studied canyons known for high cetacean abundance (Table 1); an important limitation further discussed in Section 5. Our understanding of the importance of canyon habitats to cetaceans is thus far from complete.

To conduct this review, reports of cetacean associations with submarine canyons primarily within scientific journal articles, as well as in other sources of information such as project reports, were examined. Both scientific study results and anecdotal reports of increased cetacean abundance within submarine canyons were included. Cetacean associations with the canyons reviewed were categorized according to the strength of evidence supporting the hypothesis that a greater abundance of cetaceans occur within the canyon as compared to adjacent shelf/slope areas. For the purpose of this review, data from scientific studies showing increased abundance of cetaceans within the canyon as compared to the adjacent shelf/slope area from multiple surveys collected over multiple years was considered to be strong scientific evidence of enhanced cetacean abundance within a canyon. Scientific studies showing increased abundance of cetaceans within a canyon from at least one survey of the canyon and adjacent shelf/slope area within a single year, or studies that show relatively high cetacean abundance within the canyon consistently over multiple years, were considered moderate scientific evidence of enhanced cetacean abundance within a canyon. Scientific studies that show relatively high cetacean abundance within a canyon during a single year, or anecdotal reports of high numbers of cetaceans within a canyon, were considered weak evidence of enhanced cetacean abundance within the canyon.

Twenty-one submarine canyons that appear to attract cetaceans were included in this review, which are summarized in Table 1. There was strong scientific evidence of enhanced cetacean abundance in seven of the canyons reviewed, while moderate scientific evidence existed for nine of the canyons and weak evidence was found for five of the canyons (Table 1). The following sections discuss general trends in cetacean abundance within these 21 canyons in relation to their physical characteristics and the species that tend to associate with them.

2.1. Trends in the physical characteristics of the canyons

It is apparent that the tendency for cetaceans to associate with submarine canyons is a worldwide phenomenon, with reports of relatively high cetacean abundance in canyons across the globe. For example, there is strong scientific evidence of increased cetacean abundance relative to the adjacent shelf and slope within the Gully, Shortland and Halimand canyons located off eastern Canada (Hooker et al., 1999, Whitehead, 2013; Wimmer and Whitehead, 2004), Monterey Canyon of the western United States (Croll et al., 2005; Schoenherr, 1991), Kaikoura Canyon off eastern New Zealand (Jaquet et al., 2000), Perth Canyon off southwestern Australia (Branch et al., 2007; McCauley et al., 2004; Rennie et al., 2009a, 2009b) and Genoa Canyon of the Mediterranean Sea (D'Amico et al., 2003; Moulins et al., 2007, 2008) (Table 1). Enhanced cetacean abundance and diversity is observed in canyons of varying physical characteristics. The canyons reviewed occurred on both narrow and wide continental shelves, with distance to the nearest point on land ranging from less than a kilometer to more than 250 km. The size of these canyons ranged from approximately 25 to 240 km long, and 7 to 56 km wide (as measured at the canyon mouth). Depth of these canyons ranged from about 10 to 1600 m deep at the canyon head, to *approx.* 1000 to 4300 m deep at the canyon mouth. Although some of the canyons are associated with rivers and valleys on land, and/or depositional fan valleys at the mouth of the canyon, not all of the canyons are associated with such features (Table 2). Cetaceans thus show associations with a mix of different canyon types (as defined by Harris and Whiteway, 2011).

There is some evidence that cetaceans are more likely to associate with larger submarine canyons (Wimmer and Whitehead, 2004). Most of the canyons reviewed here are of considerable size and are generally among the largest topographic features present in a particular region. For example, Barrow canyon is the largest canyon in the Beaufort Sea, Kaikoura canyon is the largest canyon off New Zealand, and Cap Breton canyon is the largest canyon in the Bay of Biscay. The best example of the positive relationship between canyon size and cetacean abundance is demonstrated by northern bottlenose whale density in the Scotian Shelf canyons off eastern Canada. During a transect study conducted along the shelf edge, the highest northern bottlenose whale sighting rates occurred in the largest of the canyons, the Gully (0.494–0.541 encounters/h), with whales sighted less often per unit time in the second largest canyon, Shortland canyon (0.289 encounters/h), and at a still lower rate in the smaller Haldimand canyon (0.138 encounters/h) (Wimmer and Whitehead, 2004). Northern bottlenose whales were not observed in the smallest Scotian Shelf canyons; Logan, Verill, Bonnechamps and Dawson canyons, and no sightings occurred outside of canyons (Wimmer and Whitehead, 2004). However, examination of sighting rates of other cetacean species within the Gully, Shortland and Haldimand canyons indicate that some species occur at similar densities in all three canyons, and sometimes even at higher densities in the smaller canyons (Whitehead, 2013). The relationship between canyon size and cetacean abundance is thus not entirely clear. Other than canyon

Table 1
Summary of cetacean associations with the 21 submarine canyons reviewed. "Species" indicates the cetacean species observed at increased abundance within the canyon. "Residence" indicates if the species likely reside in the canyon seasonally, year-round, or if this information is unknown. "Type of Evidence" indicates whether strong scientific evidence (1), moderate scientific evidence (2), or weak evidence (3) was found to support enhanced cetacean abundance within the canyon for the species listed.

Canyon	Species	Residence	Type of evidence	Description of evidence indicating enhanced cetacean abundance within canyon
The Gully (Eastern Canada)	Blue whale, fin whale, humpback whale, long-finned pilot whale, bottlenose dolphin, common dolphin, striped dolphin	Seasonal	1	Studies dating back to the 1980s including vessel-based surveys of the shelf and slope area over multiple years show significantly higher cetacean sighting rates within the Gully as compared to adjacent shelf/slope areas for a number of species (Baird et al., 1993; Gowans and Whitehead, 1995; Gowans et al., 2000; Hooker and Baird, 1999; Hooker et al., 1999, Whitehead, 2013; Whitehead et al., 1992; Wimmer and Whitehead, 2004). Northern bottlenose whale photo-identification studies over the same time period indicate that the canyon is important habitat for this species (Gowans et al., 2000; Hooker et al., 2002b; Wimmer and Whitehead, 2004).
	Northern bottlenose whale, sperm whale, Atlantic white-sided dolphin	Year-round	1	
	Sei whale, Sowerby's beaked whale	Unknown	2	
Shortland Canyon and Haldimand Canyon (Eastern Canada)	Northern bottlenose whale	Year-round	1	Vessel-based surveys of the shelf and slope area over multiple years show significantly higher northern bottlenose whale sighting rates in the canyons as compared to adjacent shelf/slope areas (Wimmer and Whitehead, 2004). Relatively high sighting rates of Sowerby's beaked whales and other cetacean species also occur within these canyons (Whitehead, 2013).
	Sowerby's beaked whales	Unknown	2	
	Blue whale, fin whale, long-finned pilot whale, common dolphin, striped dolphin, Atlantic white-sided dolphin	Seasonal	3	
Hydrographer Canyon (Eastern United States)	Fin whale, sei whale, humpback whale, North Atlantic right whale	Unknown	3	Many cetacean species have been sighted in Hydrographer Canyon including baleen whales, beaked and other toothed whales, and delphinids (CETAP, 1982), though the most notable sighting was a large number of baleen whales (> 79 individuals) observed within 15 km of the canyon during a single day of the 1980 CETAP aerial survey (Kenney and Winn, 1987).
Mississippi Canyon (Gulf of Mexico)	Sperm whales	Rear-round	3	High group encounter rates of sperm whales, bottlenose dolphins and Risso's dolphins occurred in the Mississippi Canyon during vessel-based surveys conducted between 1992 and 1994 (Baumgartner et al., 2001).It has been speculated that the canyon is an important habitat for sperm whales in the Gulf of Mexico due to their frequent occurrence near the canyon (Davis et al., 1998).
	Bottlenose dolphins, Risso's dolphins	Unknown	3	
Great Bahamas Canyon (Bahamas)	Blainville's beaked whale, dwarf sperm whale	Year-round	2	More than 13 species of odontocetes were observed in the canyon during vessel-based surveys in 2007 and 2008, with Blainville's beaked whales, dwarf sperm whales, and sperm whales being the most commonly sighted species (Claridge and Durban, 2008). Sightings of Blainville's beaked whales during vessel-based surveys in 2000 and 2002 were clustered over the canyon wall (Claridge, 2006). Dwarf sperm whales were also found to be primarily distributed over the canyon during vessel-based surveys conducted between 2001 and 2005 (Dunphy-Daly et al., 2008).
	Sperm whale	Year-round	3	
	Cuvier's and Gervais' beaked whale, pygmy sperm whale, killer whale, pygmy killer whale, short-finned pilot whale, melon-headed whale, Atlantic spotted dolphin, pantropical spotted dolphin, bottlenose dolphin, Fraser's dolphin, striped dolphin, Risso's dolphin, rough-toothed dolphin, minke whale	Unknown	3	
Little Abaco Canyon (Bahamas)	Blainville's beaked whale	Year-round	2	Vessel-based surveys between 1998 and 2001 found that sighting rates of cetaceans in the region were low overall, but most sightings occurred over the portion of Little Abaco Canyon included in the study area (MacLeod et al., 2004), and almost all Blainville's beaked whales sighted during the surveys occurred in the canyon (MacLeod and Zurr, 2005).
Monterey Canyon (western United States)	Blue whale	Seasonal	1	During vessel-based surveys conducted in 1986, large numbers of blue whales were observed over Monterey Canyon (Schoenherr, 1991), and blue whales were found to be concentrated over the edge of the canyon during surveys conducted on whale-watch vessels between 1992 and 1996 (Croll et al., 2005). During vessel-based surveys between 1996 and 1999, baleen whales, particularly humpback whales, were most commonly observed over the canyon (Benson et al., 2002). The canyon has also been noted as a preferred habitat for Dall's porpoise, while other odontocete species in Monterey Bay do not appear to associate specifically with the canyon habitat (Yen et al., 2004).
	Humpback whale	Seasonal	2	
	Gray whale, Dall's porpoise	Seasonal	3	
Zhemchug Canyon (Bering Sea)	Fin whale	Seasonal	3	Vessel-based surveys in 1999 show fin whale sightings clustered around the outer shelf break especially near Zhemchug Canyon (Moore et al., 2000b).

Table 1 (*continued*)

Canyon	Species	Residence	Type of evidence	Description of evidence indicating enhanced cetacean abundance within canyon
Pribilof Canyon (Bering Sea)	Fin whale, Dall's porpoise Baird's beaked whale	Seasonal Unknown	2 3	Vessel-based surveys in 1999 and 2000 show fin whale sightings clustered around Pribilof Canyon (as well as other areas on the shelf edge and in the middle shelf). Sightings of Dall's porpoise were also relatively common around the canyon, and the only beaked whale sighting recorded during the surveys was in the canyon (Moore et al., 2002).
Barrow Canyon (Beaufort Sea)	Beluga whale	Seasonal	2	Aerial surveys between 1982 and 1991 indicate that beluga whales preferentially select steep slope habitat associated with Barrow Canyon throughout the fall, although they were also commonly observed in adjacent slope areas (Moore et al., 2000a).
Mackenzie Canyon (Beaufort Sea)	Beluga whale, bowhead whale	Seasonal	3	During vessel-based surveys in 2002, the only two beluga whales sighted were in Mackenzie Canyon. Some bowhead whales were also sighted in the canyon (Harwood et al., 2005). Of 12 bowhead whales equipped with satellite tags in 2002, two individuals spent most of their time undergoing long, deep dives in Mackenzie Canyon, and a third individual also spent time in the canyon (Kruitzikowsky and Mate, 2000).
Kaikoura Canyon (Eastern New Zealand)	Sperm whale Dusky dolphin	Year-round Year-round	1 3	Vessel-based surveys between 1990 and 1997 show high numbers of sperm whales occurring in the canyon, although distribution varied seasonally with the whales concentrating in the canyon during summer and becoming more evenly distributed throughout the area during winter. Individuals have been resighted in the canyon within the same year and over several years (Jaquet et al., 2000). Large groups of dusky dolphins are known to be attracted to the canyon year-round, and active-acoustic surveys conducted in 2002 showed that the dolphins feed on deep-scattering layers within the canyon at night (Benoit-Bird et al., 2004).
Perth Canyon (Southwestern Australia)	Pygmy blue whales	Seasonal	1	Acoustic, aerial, and vessel-based surveys conducted over several years found relatively high concentrations of pygmy blue whales within the canyon throughout the summer as compared to the adjacent shelf areas, and the canyon has been identified as a feeding area for these whales (Branch et al., 2007; McCauley et al., 2004; Rennie et al., 2009a, 2009b).
Swatch of No Ground (Bay of Bengal)	Indo-Pacific dolphins Bryde's whale	Unknown Unknown	2 3	A vessel-based survey in 2004 recorded relatively large groups of Indo-Pacific dolphins in the canyon (Smith et al., 2008), and two winters of photo-identification studies recorded large numbers of individuals within the canyon and indicates that the canyon is a particularly suitable habitat for the population (Mansur et al., 2012). The only two confirmed Bryde's whale sightings during the 2004 survey occurred in the canyon (Smith et al., 2008).
Trincomalee Canyon (Sri Lanka)	Blue whale, sperm whale	Unknown	2	Two years of vessel-based sperm whale surveys indicate that a particularly high concentration of sperm whales occur at the mouth of Trincomalee Bay in Trincomalee Canyon (Gordon, 1991). Opportunistic sightings of other species during these surveys also indicate a concentration of blue whales in the canyon during both years (Alling et al., 1991).
Genoa Canyon (Mediterranean Sea)	Cuvier's beaked whale Striped dolphins, Risso's dolphins, sperm whales	Year-round Unknown	1 3	During vessel-based surveys in 1999 and 2000, Cuvier's beaked whales were only observed in Genoa Canyon (D'Amico et al., 2003), and these whales were significantly more abundant in the canyon as compared to adjacent shelf/slope areas during vessel-based surveys conducted between 2004 and 2006 (Moulins et al., 2008). Cuvier's beaked whale sightings collected from various datasets between 2000 and 2006 indicate that the whales aggregate in particular areas of the canyon (Moulins et al., 2007). Striped dolphins, Risso's dolphins and sperm whales were also sighted more frequently than expected within some areas of the canyon (Moulins et al., 2008).
Cuma Canyon (Mediterranean Sea)	Fin whale, common dolphin Bottlenose dolphin, Risso's dolphin, striped dolphin, sperm whale	Seasonal Unknown	2 3	Vessel-based surveys conducted in waters off Ischia between 1991 and 2000 indicate a concentration of cetaceans in Cuma Canyon (Mussi et al., 1999). During studies focused in the canyon between 1996 and 2000, fin

Table 1 (*continued*)

Canyon	Species	Residence	Type of evidence	Description of evidence indicating enhanced cetacean abundance within canyon
				whales were the species most regularly sighted in the canyon (Mussi et al., 1999). Most common dolphin sightings recorded between 1997 and 2001 occurred in the canyon, and individuals have been re-sighted in the canyon over different years during photo identification studies (Mussi et al., 2002).The canyon has been identified as one of the key areas of distribution for common dolphins in the Mediterranean Sea (Bearzi et al., 2003). Sperm whales, which are poorly known in the area, have also been sighted in the canyon (Mussi et al., 2005).
Cap Breton Canyon (Western Europe)	Cuvier's beaked whale	Year-round	2	In the Bay of Biscay, Cuvier's beaked whales show a habitat preference for Cap Breton Canyon (Williams et al., 1999). 90% of Cuvier's beaked whale sightings during shipboard cetacean surveys in the Bay of Biscay between 1995 and 2006 occurred in the canyon (Smith 2010). Sightings of northern bottlenose whales and Sowerby's beaked whales also occurred predominantly in the canyon (Smith, 2010), and several other species were frequently sighted in the canyon (Certain et al., 2008; Smith 2010).
	Northern bottlenose whale, Sowerby's beaked whale	Unknown	2	
Santander Canyon (Western Europe)	Beaked whales	Unknown	3	Beaked whale sightings compiled by MacLeod (2004) indicate that the Bay of Biscay in general is a beaked whale hotspot, and that Santander Canyon appears to be particularly important beaked whale habitat.
Bleik Canyon (Western Europe)	Sperm whale, long-finned pilot whale,	Unknown	2	Ciano and Huele (2001) note that whale-watch vessels have been reporting opportunistic sightings of sperm whales in Bleik Canyon since the 1980s. During the 1998 whale-watch season, of 61 sperm whales were photographically identified, 32 were resightings from previous years (Ciano and Huele, 2001). Long-finned pilot whales have been sighted by the whale-watch vessel in the canyon in most years since the 1980s, and there have also been infrequent sightings of humpback whales (Ciano and Jørgensen, 2000).
	Humpback whale	Unknown	3	

size, there were no obvious common physical features shared by all of the canyons reviewed (Table 2).

Larger canyons are known to have a more pronounced effect on circulation patterns, creating more area for vertical mixing of the water column and shelf/slope water exchange (Hickey, 1995). This could result in increased cetacean prey abundance through various mechanisms such as up-canyon flow, upwelling, down-canyon flow, and downwelling (see Section 3). However, this apparent positive relationship between canyon size and cetacean abundance could also be due to the limited amount of data available on smaller canyons and therefore needs to be further investigated.

2.2. Trends in cetacean species that associate with the canyons

Many cetacean species appear to be attracted to submarine canyons including baleen whales, toothed whales and dolphins. Several of the canyons reviewed appear to attract a high diversity of species (as was the case for the eastern Canadian canyons and the Great Bahamas Canyon; Table 1). Species associations with canyons may vary over time (seasonally), or are consistent over long periods (year-round residency). In some cases, certain species occur within a canyon seasonally, while other species are observed in the same canyon throughout the year (Table 1). Sometimes individual whales are observed in the same canyon over multiple years (Ciano and Huele, 2001; Gowans and Whitehead, 2001; Jaquet et al., 2000).

Baleen whales do not appear to associate with canyons as strongly as toothed whales. Baleen whales associated with 14 of the canyons reviewed. There was strong scientific evidence for increased baleen whale abundance within the canyon for three of the canyons reviewed, moderate scientific evidence for three of the canyons, and only weak evidence for eight of the canyons. Baleen whales only appear to associate with canyons seasonally (Table 1).

Conversely, toothed whales associated with 18 of the canyons reviewed, with strong scientific evidence presented for five canyons, moderate scientific evidence for nine canyons and weak evidence for four canyons (Table 1). Sperm whales (*Physeter macrocephalus*) were the species that most commonly associated with the canyons, with evidence of increased sperm whale abundance within nine canyons (strong scientific evidence for two canyons, moderate scientific evidence for two canyons and weak evidence for five canyons; Table 1). Beaked whales were found to associate with nine of the canyons reviewed (strong scientific evidence for four canyons, moderate scientific evidence for three canyons and weak evidence for two canyons; Table 1). While some toothed whale species, particularly dolphins, appeared to only associate with canyons seasonally, beaked whales, sperm whales, dwarf sperm whales (*Kogia sima*), and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) associated with canyons year-round (Table 1).

It is important to note that in addition to processes occurring within the canyon itself, the life history and annual movement patterns exhibited by a species will also likely influence whether they associate with a canyon seasonally or year-round. For example, the seasonal associations of baleen whales with canyons may be a reflection of the tendency for baleen whales to undergo extensive seasonal migrations (Bowen and Siniff, 1999). It is interesting that the cetaceans which associate with canyons on a seasonal basis (baleen whales and dolphins) tend to feed primarily on shallow-water prey such as euphasiids, small fish and invertebrates (Bowen and Siniff, 1999; Gaskin, 1982). The species that most often associate

Table 2
Physical characteristics of the 21 submarine canyons reviewed. "Dist. from shore" is the approximate distance from the canyon head to the nearest point on land, "Lenth" is the estimated length of the canyon from the canyon head to the base of the continental slope, and "Width" is the estimated width of the canyon at the canyon mouth. The information presented in this table was obtained from the literature reviewed or from measurements made on bathymetric charts.

Canyon	Dist. from shore (km)	Length (km)	Width (km)	Depth at head (m)	Depth at mouth (m)	Associated river/feature on land	Associated fan valley
The Gully (Eastern Canada)	200	40	16	50	> 2500	None	None
Shortland Canyon (Eastern Canada)	220	27	13	50	> 1000	None	None
Haldimand Canyon (Eastern Canada)	220	20	10	50	> 1000	None	None
Hydrographer Canyon (Eastern United States)	180	50	10	140	2010	None	Hydrographer Fan Valley
Mississippi Canyon (Gulf of Mexico)	45	> 120	7	90	> 1500	Mississippi River	Mississippi Fan
Great Bahamas Canyon (Bahamas)	25	230	37	1400	4270	None	None
Little Abaco Canyon (Bahamas)	25	25	7	1600	> 3900	None	None
Monterey Canyon (Western United States)	0.03	111	20	15	2900	Salinas and Pajaro Rivers	Monterey Fan Valley
Pribilof Canyon (Bering Sea)	500	160	56	150	2360	None	Unknown
Zhemchug Canyon (Bering Sea)	500	160	100	150	> 2700	None	Unknown
Barrow Canyon (Beaufort Sea)	30	240	24	100	> 1000	None	Unknown
Mackenzie canyon (Beaufort Sea)	20	10	150	50	300	Mackenzie and Firth Rivers	None
Kaikioura Canyon (Eastern New Zealand)	1.5	60	17	18	2000	Multiple rivers and land valleys	Hikurangi Trench
Perth Canyon (Southwestern Australia)	10	100	20	50	4000	Swan River System	Unknown
Swatch of No Ground (Bay of Bangal)	10	200	20	–	> 1200	Ganges-Brahmaputra-Meghna Rivers	Bengal fan
Trimcomalee Canyon (Sri Lanka)	0.18	37	7.4	10	2900	Trincomalee and Koddiyar Bay	None
Genoa Canyon (Mediterranean Sea)	< 1	40	20	80	1910	Polcevera River	Unknown
Cuma Canyon (Mediterranean Sea)	< 20	> 100	15	300	> 3000	None	Unknown
Cap Breton Canyon (Western Europe)	0.3	250	37	120	3990	Adour River	Yes
Santander Canyon (Western Europe)	20	70	10	500	> 3000	De Boo, San Salvador, Miera Rivers	Unknown
Bleik Canyon (Western Europe)	20	40	25	200	> 1000	None	Unknown

with canyons on a year-round basis, most notably beaked and sperm whales, feed primarily on deep-water squid (Bowen and Siniff, 1999; Gaskin, 1982).

3. Processes by which submarine canyons may attract cetaceans

Cetaceans may aggregate within an area for various reasons such as for mating, giving birth to and rearing young, socializing and feeding. However, it is generally accepted that prey availability greatly influences cetacean distribution (Bowen and Siniff, 1999; Gaskin, 1982; Stevick, et al., 2002). Enhanced prey density is often used to explain increased cetacean abundance within submarine canyons (*e.g.,* Genin, 2004; Hooker et al., 2002a; Yen et al., 2004).

As a consequence of following prey, the occurrence of cetaceans within an area tends to be indirectly related to environmental variables and oceanographic features that affect the distribution and abundance of their prey (*e.g.,* Hastie et al., 2004; Jaquet, 1996; Jaquet and Whitehead, 1996; Smith and Whitehead, 1993). Euphausiids, copepods, fish and squid are common cetacean prey (Bowen and Siniff, 1999; Gaskin, 1982). Identifying processes that increase the density of these organisms is important for understanding the factors that influence cetacean distribution within an area or around specific features such as submarine canyons. Physical features that enhance primary productivity and convert it to prey biomass over short temporal and spatial scales, that concentrate prey through physical mechanisms, or make prey more accessible at the surface are likely to be important habitat for cetaceans (Baumgartner et al., 2001). Submarine canyons have been linked to all of these processes.

3.1. How the continental slope in general enhances cetacean prey density

The distribution of cetaceans is linked to the continental slope in general in some areas (*e.g.,* Azzellino et al., 2008; Moore et al., 2000b; Selzer and Payne, 1988). Physical features of the continental slope, specifically depth and seafloor relief, are known to affect the distribution, abundance and density of these types of organisms in the following ways.

Shelf-break upwelling occurs when circulation patterns interact with the steep bottom relief of the continental slope causing an onshore transport of deep water (Bakun, 1996; Owen, 1981). This results in increased nutrient levels within surface waters which sustains higher phytoplankton abundance and increases primary productivity. This in turn supports greater numbers of zooplankton, fish, squid, and the top-level predators that feed on these organisms (Bakun, 1996).

Shelf-break or upwelling fronts that form over or near the continental slope separate more saline shelf waters caused by upwelling from less dense offshore waters (Owen, 1981). The boundary between these different water masses is usually associated with a zone of convergent flow where the water mass of greater density sinks below the less dense water mass, resulting in an area of downwelling (Bakun, 1996; Owen, 1981). Weak-swimming organisms concentrate along these downwelling convergence zones, which may act as a physical barrier to their horizontal movement (Bakun, 1996; Cañadas et al., 2003; Graham et al., 1992). High concentrations of euphausiids are commonly recorded at upwelling fronts (Barrange, 1994; Genin, 2004; Lavoie et al., 2000; Schoenherr, 1991; Simard et al., 1986). Fronts also appear to be important factors that contribute to squid biomass (Uda, 1959; Zuev and Nesis, 1971), and it has been speculated that upwelling fronts concentrate larval squid and more passive squid

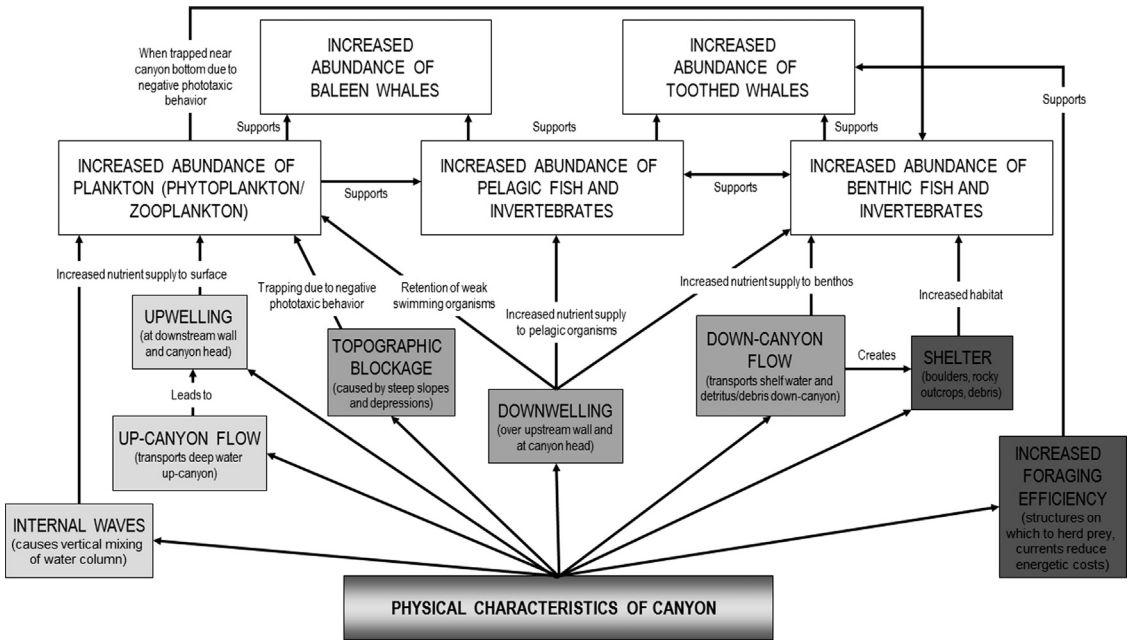

Fig. 1. Summary of mechanisms through which submarine canyons may attract cetaceans. Light gray boxes indicate enrichment processes, medium gray boxes indicate concentrating processes and dark gray boxes indicate aggregating processes.

species along convergence zones (Jaquet and Whitehead, 1996; Smith and Whitehead, 1993). High concentrations of zooplankton and other weak-swimming organisms along fronts are known to attract organisms of successively higher tropic levels (Bakun, 1996; Cañadas et al., 2003; Graham et al., 1992; Owen, 1981).

Downwelling at convergence zones along the shelf-break can transfer surface biomass and oxygen into deep ocean waters, increasing the amount of nutrients and organic material available to the benthos and deep-water fish and invertebrates. Typically, a decline in the abundance and biomass of benthic and demersal organisms is expected as depth increases as a result of a decreasing amount of food reaching the benthos (Cañadas et al., 2003; Haedrich et al., 1980; Houston and Haedrich, 1984; Thiel, 1979; Wolff, 1977). Deep-water pelagic species depend on a rain of organic matter from the surface for sustenance and their abundance is therefore affected by the quantity of nutrients reaching deeper layers of the water column (Rowe, 1981). In shelf-break regions where the export of detritus from surface waters into deep water is enhanced, a greater abundance of benthic, demersal and deep-water pelagic species can be supported (Baumgartner et al., 2001; Houston and Haedrich, 1984), which in turn attract organisms of higher tropic levels.

It is clear that steep seafloor relief of the continental slopes can influence circulation patterns in ways that increase cetacean prey abundance and density. It is therefore reasonable to expect that submarine canyons also have an enhanced effect on the abundance and density of prey due to a concentration of slope habitat within a relatively small area. The following sections describe general circulation and flow patterns occurring within and around submarine canyons and discuss specific mechanisms through which submarine canyons may enhance cetacean prey abundance and density as a result of these flow patterns. These mechanisms are categorized into three processes that are summarized in Fig. 1: enrichment processes, concentrating processes and aggregating processes. These three processes tend to act on different trophic levels and by no means are completely separate from one another. In many cases, several different mechanisms likely work together to increase cetacean prey abundance and density within a submarine canyon.

3.2. Flow patterns within and around submarine canyons

Both downwelling and upwelling zones are known to occur in submarine canyons. There is generally a downwelling zone at the rim of the canyon (the edge where the shelf-floor meets the steep wall of the canyon) on the upstream side of the canyon (the side which flowing water reaches first), where water near the floor of the continental shelf flows over the canyon rim and down into the canyon. The water flowing into the canyon then typically turns towards the head of the canyon (up-canyon) until it reaches the downstream rim and is forced back up onto the shelf, creating a zone of upwelling, and sometimes an eddy (Allen, 1996; Allen and Hickey, 2010; Allen et al., 2001; Hickey, 1995, 1997; Klinck, 1996). Upwelling may also occur over the downstream wall at the head of the canyon as a result of water flowing along the continental slope turning into the canyon and being forced up the sloping bottom as it follows the canyon isobaths (Allen et al., 2001; Hickey, 1995; Klinck, 1996). Deep water flowing near the base of the continental slope tends to turn into the canyon and either follows the canyon isobaths around the entire canyon and flows out the opposite side in wider canyons, or turns in a circular flow pattern within the canyon in narrower canyons (Allen et al., 2001; Hickey, 1995; Klinck, 1996).

The strength of upwelling or downwelling within a canyon will generally vary over time. Upwelling-favorable conditions such as the presence of shelf-break upwelling, an onshore pressure gradient and left-bounded alongshore flow (coast is to the left when looking downstream) in the northern hemisphere or right-bounded alongshore flow in the southern hemisphere, or certain directions of ice movement relative to the canyon (relevant for some Arctic canyons, *e.g.*, Williams et al., 2006), accelerates up-canyon flow and increases the volume of water upwelling at the canyon head. The presence of an offshore pressure gradient and right-bounded alongshore flow in the northern hemisphere or left-bounded alongshore flow in the southern hemisphere correspond to downwelling-favorable conditions which result in a weakening of up-canyon flow and allow for increased flow down-canyon (Hickey, 1997; Klinck, 1996). Often mean flow measured along the axis of submarine canyons over several

months does not appear to follow any predictable pattern; sometimes the flow is mainly up-canyon, sometimes it is mainly down-canyon, and frequently the flow occurs both up- and down-canyon simultaneously (Hickey, 1995). Flow in opposite directions on either side of a canyon may create large low-flow retention zones in the middle of the canyon (Rutherford and Breeze, 2002). Cyclonic and anticyclonic eddies have also been known to develop within canyons (Allen, 1996; Allen and Durrieu de Madron, 2009; Hickey, 1997).

In addition to creating upwelling and downwelling zones, the steep topography of submarine canyons can enhance internal tides or generate or amplify internal waves. Internal waves and tides may break within the canyon and create turbulence, increasing vertical mixing of the water column (Allen and Durrieu de Madron, 2009; Hickey, 1995; Kunze et al., 2002). Friction generated by water flowing around the canyon topography can cause water turbulence in the bottom boundary layer near the head of some canyons, also increasing vertical mixing of the water column (Hickey, 1995).

It is important to note that most of our knowledge of flow patterns within and around submarine canyons is based on limited data and comes from field observations within a few well-studied canyons or is inferred from modeling studies. In most cases, oceanographic data have not been collected under all possible environmental conditions throughout the year; thus, our understanding of flow patterns around these features is incomplete. Flow patterns within canyons are likely to be more complex than described above and probably vary greatly with canyon size, shape, depth, location and local circulation patterns.

3.3. Enrichment processes

Enrichment processes were considered to be processes that "enrich" or supply nutrients to the photic zone, thereby supporting increased primary productivity levels. Within submarine canyons this includes processes that cause upwelling or increase vertical mixing of the water column. Increased primary productivity caused by topographically induced upwelling has been used to explain increased biological diversity in the vicinity of canyons (Hickey, 1995). As described above, up-canyon flow caused by water circulation patterns, wind, or ice-movement may cause upwelling at the head of a canyon (Allen et al., 2001; Hickey, 1995; Klinck, 1996; Williams et al., 2006). Cyclonic eddies that upwell deep water to the surface may also develop within canyons (Allen et al., 2001; Hickey, 1995; Klinck, 1996; Rennie et al., 2009a). Internal waves, tides and turbulence generated by canyon topography can enhance vertical mixing of the water column, resulting in increased concentrations of suspended particles within the canyon relative to the adjacent slope (Hickey, 1995; Kunze et al., 2002). A consistent source of nutrients in surface waters supports increased primary productivity and may increase phytoplankton abundance within and around a canyon, in turn increasing the abundance of zooplankton and micronekton (including euphausiids, which are the primary prey of some baleen whales). Increased abundance of these organisms attracts other organisms such as pelagic fish (Bakun, 1996), which baleen whales also feed upon. Enrichment processes therefore attract baleen whales to submarine canyons (Fig. 1). Additionally, pelagic fish and invertebrates (such as squid) are the primary prey of toothed whales; thus, increased abundance of these organisms can attract toothed whales to submarine canyons (Fig. 1).

It is important to note that in order for enrichment processes to impact higher levels of the food chain within a canyon, they have to be sustained within the canyon over a relatively long period of time (Genin, 2004; Yen et al., 2004). Temporary upwelling zones will bring nutrients to the surface, but if the upwelling is not maintained currents tend to transport the nutrients away from the area before the energy is transferred up the food chain. It is typical for upwelled water to become progressively richer in phytoplankton and zooplankton as it is transported away from the zone of upwelling (Bakun, 1996). Upwelling within a canyon will therefore only result in increased cetacean abundance (and in particular increased abundance of toothed whales who feed on higher levels of the food chain) near the canyon if the upwelling is persistent for periods of weeks to months (Genin, 2004). Indeed, some canyons are known to promote nutrient exchange between waters of the continental shelf and deep-ocean, increasing productivity on the nearby continental shelf by making deep nutrient-rich water accessible to the near-shore zone (Hickey, 1995) rather than increasing productivity within the canyon itself. It is likely that enrichment processes can occur within a canyon throughout the year but are probably more important seasonally, such as during the spring, summer and fall, when light levels increase and shelf-break upwelling occurs.

3.4. Concentrating processes

Concentrating processes were considered to be processes that concentrate passive or weakly swimming organisms or organic material. General downwelling and downwelling convergence zones are both mechanisms known to occur within submarine canyons (Genin, 2004; Hickey, 1997; Klinck, 1996). It has been suggested that sinking plankton-rich waters at such zones within canyons may provide a source of food for larger deep-water organisms such as squid and fish (Jaquet, 1996). Concentrations of zooplankton and micronekton at convergence zones may attract baleen whales, while aggregations of benthic and pelagic fish and invertebrates may attract toothed whales (Fig. 1). Some cetacean species, such as sperm whales, have been found to be more abundant at downwelling zones rather than at upwelling zones (Jaquet, 1996). Low-flow retention zones in the middle of the canyon created by bidirectional or circular flow patterns within in the canyon (*e.g.,* Rutherford and Breeze, 2002) also act as a prey-concentrating mechanism.

In addition to flow patterns within canyons, the behavior of zooplankton and micronekton can result in large concentrations of prey within a canyon. Many of these organisms display negative phototactic behavior, migrating into deeper waters during the day to avoid illumination (and hence predation) and rising to the surface at night to feed. This vertical migration behavior can result in large concentrations of zooplankton and micronekton on the shelf-floor. When this occurs near canyons, currents may funnel animals near the shelf-floor into the canyon, concentrating these organisms near the bottom of the canyon (Greene et al., 1988). This may be an especially important mechanism in cases where there is an enhanced near-bottom current just outside of the canyon and during downwelling-favorable conditions when up-canyon flow is weakened and upwelling decreases, allowing for increased down-canyon flow (Hickey, 1997; Klinck, 1996). It has been suggested that oceanic migratory micronekton that accumulates within the heads of some canyons is the result of passive transport of these organisms into the canyons by local currents (*e.g.,* Macquart-Moulin and Patriti, 1996). The intensity of the concentration of the micronekton on the upper slope at the head of these canyons appears to be positively correlated with depth of the diurnal migration pattern of the different micronekton species (Macquart-Moulin and Patriti, 1996). As well as being swept into the canyon, zooplankton and micronekton may actively migrate into the deeper canyon waters to avoid illuminated shelf waters during the day. In this way, canyons may act as traps that accumulate smaller organisms that migrate to deeper depths in the morning after they have traveled over the shelf during nocturnal horizontal migrations, a process called "topographic blockage" (Genin, 2004; Macquart-Moulin and Patriti, 1996). Topographic blockage may attract baleen whales to the canyon to feed on these

large concentrations of zooplankton and/or micrnekton. These large concentrations may also attract benthic and pelagic fish and invertebrates, which in turn may attract toothed whales (Fig. 1).

Downwelling and down-canyon flow patterns can also concentrate organisms by increasing secondary productivity within a canyon, making organic matter more accessible to deep-water fish and invertebrates. Submarine canyons tend to have higher sedimentation rates than surrounding shelf regions (Houston and Haedrich, 1984), and many canyons cut landward across the shelf sufficiently far to interrupt the movement of river-supplied sediment along the shelf. Sediment traps have been used to demonstrate that particles concentrate in canyons following re-suspension on the adjacent shelf (Hickey, 1995). Enhanced abundance of benthic and demersal organisms is found in areas where there is an influx of organic debris (Houston and Haedrich, 1984). During times of down-canyon flow, canyons serve as channels for energetic currents and turbidity flows and thus act as conduits for the transport of accumulated sediment and detritus from the shelf to the deep ocean. Therefore, whereas up-canyon flow can transfer nutrients from deep offshore waters onto the shelf, down-canyon flow can transfer sediment and organic debris from shelf waters into the deeper waters of the canyon (Levin and Gooday, 2003). Extensive accumulations of sediments and detritus have been observed on the floor of some submarine canyons, forming a persistent mat of organic and inorganic debris (*e.g.,* Harold et al., 1998; Lewis and Barnes 1999; Vetter and Dayton, 1998, 1999). The presence of organic debris within canyons has been shown to affect community biomass, size, and structure (Houston and Haedrich, 1984), often enhancing the abundance of benthic organisms relative to the adjacent slope (Cartes and Sardà, 1993; Haedrich et al., 1980; Vetter and Dayton, 1998, 1999). In general, suspension feeders benefit from increased flow rate, accelerated currents, and the influx of organic debris in canyons, while elevated sedimentation rates and accumulation of macrophytic debris benefit detritivores (Vetter and Dayton 1998, 1999). The support of the lower-trophic levels and increased numbers of detritivores, planktivores and particle feeders result in a greater food supply for higher trophic levels (Levin and Gooday, 2003) such as pelagic fish and invertebrates, which toothed whales may feed upon (Fig. 1).

It is possible that concentrating processes can occur concurrently with enrichment processes, resulting in increased abundance and retention of cetacean prey within a canyon. For example, if nutrient levels on the shelf or within a canyon become augmented during periods of shelf-break upwelling, the abundance of plankton may increase which could then become concentrated in downwelling zones within the canyon (Fig. 1). In cases where the concentration of organisms within a canyon is closely tied to seasonal enrichment processes, it is likely that concentrating processes within the canyon are important seasonally. However, concentrating processes also likely occur in submarine canyons even in the absence of enrichment processes and therefore may also be important for enhancing cetacean prey abundance throughout the year.

3.5. Aggregating processes

Aggregating processes were considered to be processes that result in organisms actively moving into an area for reasons other than increased prey abundance and density (not as a consequence of increased primary productivity or the passive concentration of organisms and organic material), such as to take advantage of certain habitat types or for socializing or breeding purposes. For example, submarine canyons may attract fish and invertebrates by providing increased habitat diversity and shelter. Canyons typically have highly heterogeneous substrata (such as rocky outcrops) relative to similar depths on the adjacent continental slope, thus contributing to habitat diversity of the slope (Levin and Gooday, 2003). Increased habitat diversity may attract benthic and demersal fish and invertebrates seeking shelter, which may support pelagic fish and invertebrates and attract baleen and toothed whales (Fig. 1). As an example, increased abundance of fish species in La Jolla and Scripps canyon have been partially attributed to increased shelter provided by rock walls, boulders and patches of detritus in the canyon (Vetter and Dayton, 1999).

The physical characteristics of some canyons may increase the foraging success of cetaceans. High relief and sloping walls of canyons could potentially provide structures on which cetaceans can herd prey, or may produce currents that reduce the energetic costs of diving. Dunphy-Daly et al. (2008) suggest that physical characteristics such as these, which can increase foraging efficiency, may make canyons more attractive habitat to cetaceans (Fig. 1). It has also been suggested that upper trophic level marine predators such as cetaceans may use topographic features such as canyons as a means of predicting important foraging habitats (Yen et al., 2004), and that canyons provide navigational cues to cetaceans that facilitate feeding (Selzer and Payne, 1988).

3.6. Processes occurring in the canyons reviewed

Not all of the processes described above have been studied in all of the canyons reviewed and only very little or incomplete information is available on the circulation patterns that occur within many of these canyons. The flow patterns within and around the different canyons are highly variable likely as a result of the differences in their physical characteristics (Table 2), thus the mechanisms leading to increased cetacean abundance are expected to vary from canyon to canyon.

While enrichment, concentrating and aggregating processes likely all play a role to some degree in attracting cetaceans to any submarine canyon, particular processes seem to be especially important for attracting cetaceans to some canyons. For example, enrichment processes appear to be the driving force behind increased cetacean abundance in Perth canyon (Rennie et al., 2009a, 2009b), while concentrating processes appear to be much more important in Monterey Canyon (Graham et al., 1992). Enrichment processes may be sufficient enough on their own to attract baleen whales to canyons, particularly during periods of shelf-break upwelling when vertical mixing of the water column is sustained over long periods of time. Concentrating processes such as fronts and retention zones, and topographic blockage also likely play a key role in attracting baleen whales to canyons, especially when these processes are combined with processes that enhance vertical mixing of the water column such as upwelling. Toothed whales are more likely to be attracted to canyons through concentrating processes such as down-canyon flow and downwelling that concentrate prey or enhance secondary productivity throughout the water column including near the floor of the canyon (Fig. 1). Section 4 provides a detailed review of the Gully, a particularly well-studied canyon that likely attracts cetaceans through a variety of mechanisms.

4. The Gully Marine Protected Area

The Gully is the largest submarine canyon off eastern North America and is the most dominant topographic feature of the Scotian Slope, located south of Nova Scotia, Canada. Geological, oceanographic and biological research has been ongoing in this canyon for decades and it is one of the most studied deep-sea ecosystems off eastern Canada (*e.g.,* Gordon and Fenton, 2002; Harrison and Fenton, 1998). The Gully is characterized by a diversity of habitats and marine life. It has the highest known diversity of corals in Atlantic Canada

(Cogswell et al., 2009), has a relatively high diversity of bathyl epibenthic megafauna (Kenchington et al., 2014) and dermersal finfish, may be important spawning grounds for some marine fish (Zwanenburg, 1998), and has greater overall biomass, abundance and diversity of larger pelagic crustaceans, including numerous rare species not previously observed in Canadian waters, than adjacent slope waters (MacIsaac et al., 2014). The Gully is also known for a high diversity and abundance of cetaceans and it has been suggested that this may be one of the most important cetacean habitats on the Scotian Shelf (Whitehead et al., 1998). The ecological importance of the Gully was formally recognized in 2004 when it was named a Marine Protected Area by Canadian law (DFO, 2004).

Cetacean-focused studies have been conducted in the Gully since 1986 and more than 14 species of cetaceans have been documented within the canyon including several baleen whale species, numerous delphinids, sperm whales and three species of beaked whales (Hooker et al., 1999; Whitehead, 2013). Some of the species observed in the Gully have not been documented in adjacent shelf areas, and sighting rates of most species are significantly higher in the Gully as compared to other parts of the Scotian Shelf (Baird et al., 1993; Gowans and Whitehead, 1995; Gowans et al., 2000; Hooker and Baird, 1999; Hooker et al., 1999; Whitehead et al., 1992; Wimmer and Whitehead, 2004). Studies over the past 27 years provide strong scientific evidence that the Gully has higher cetacean diversity and abundance than adjacent shelf waters.

The Gully is particularly important habitat for northern bottlenose whales (*Hyperoodon ampullatus*). It is one of the few areas in the Northwestern Atlantic where northern bottlenose whales are consistently observed and is the southernmost location where this species regularly occurs. The northern bottlenose whales of the Gully are part of a distinct population known as the Scotian Shelf population, which consists of approximately 160 individuals (Whitehead and Wimmer, 2005) and is considered Endangered (DFO, 2010). Of more than 1500 sightings of northern bottlenose whales reported in the Scotian Shelf region dating back to the 1960s, the majority (~74%) have occurred in the Gully (Fig. 2), though it is important to note that the majority of effort in searching for these whales has also occurred in the Gully. It has been estimated that 33% of the Scotian Shelf population can be found in the Gully at any one time (Gowans et al., 2000). Northern bottlenose whales are also consistently observed in the nearby Shortland and Haldimand canyons located 50 km and 100 km to the east of the Gully, respectively; however, only about 10% of reported northern bottlenose whale sightings in the Scotian Shelf region have occurred in these two canyons (Fig. 2). As described in Section 2.1, sighting rates of northern bottlenose whales are highest in the Gully and decrease in the smaller Shortland and Haldimand canyons (Wimmer and Whitehead, 2004). Northern bottlenose whales are known to move regularly between these three canyons (Wimmer and Whitehead, 2004), though very few sightings have occurred outside of the canyons (Fig. 2). Recent acoustic monitoring studies have confirmed that the whales reside in these three canyons on a year-round basis, and that they forage in the canyons throughout the year (Moors, 2012). It is thought that an abundant and reliable source of food, namely, *Gonatus*

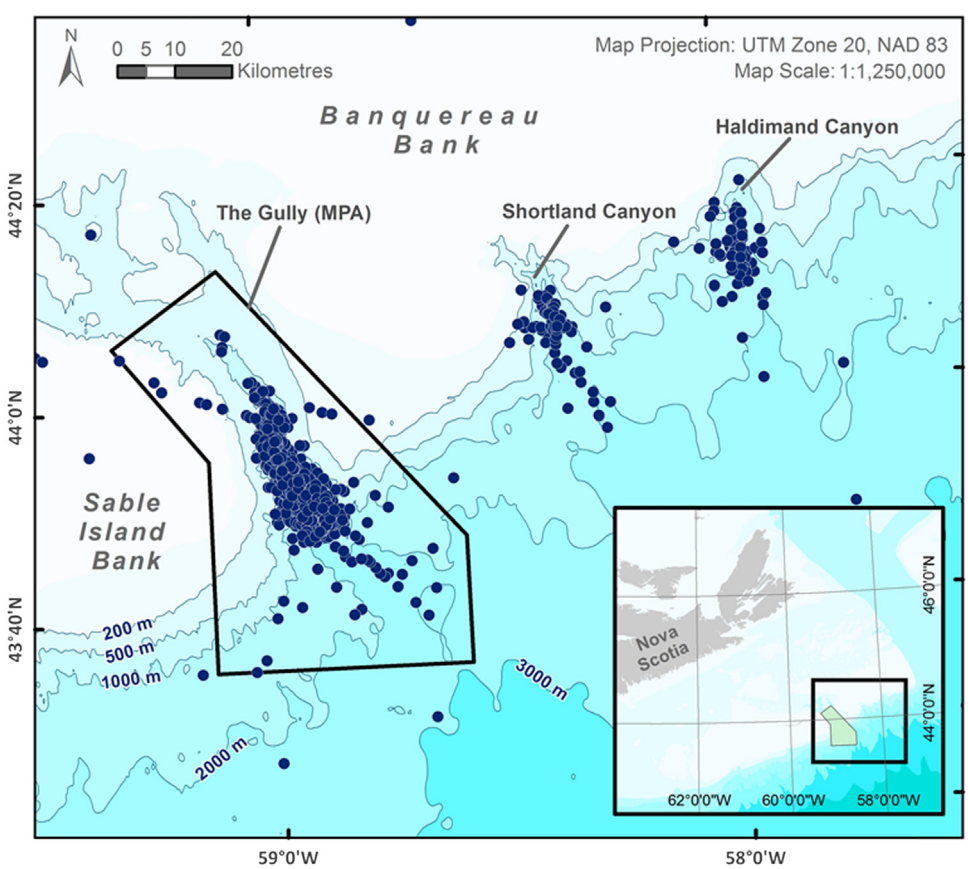

Fig. 2. Documented northern bottlenose whale sightings (filled-in circles) around the canyons of the eastern Scotian Slope between 1967 and 2010. The outer boundary of the Gully MPA is shown. Note that effort is not accounted for in this figure, nor is the effort equally distributed throughout the area captured by this figure. Data were obtained from various sources including primarily the Whitehead Lab at Dalhousie University, but also the Department of Fisheries and Oceans, fishery observers, marine mammal observers, US marine mammal surveys and whaling records. Though not all of these sightings have been confirmed, the majority were obtained from reliable sources and are likely to be accurate.

squid (the primary prey of northern bottlenose whales), must occur in the Gully in order to support the population (Hooker et al., 2002a), though little is known about squid distribution and abundance in the region. The Gully, Shortland and Haldimand canyons have all been identified as critical habitat of the Scotian Shelf northern bottlenose whale population and are protected by the Canadian Species at Risk Act (DFO, 2010).

The distribution of the various cetacean species that use the Gully is not uniform throughout the canyon. For example, minke whales (*Balaenoptera acutorostrata*) only occurred in shallow waters at the head of the canyon, sperm whales occurred throughout the canyon with the highest sighting rates at the head of the canyon, Atlantic white-sided dolphins also occurred throughout the canyon but with the highest sighting rates at the canyon mouth, and striped dolphins (*Stenella coeruleoalba*) preferred deep waters at the canyon mouth (Hooker et al., 1999). Northern bottlenose whales are known to occur in the deepest parts of the canyon, along the canyon axis in areas where water depths exceed 800 m (Hooker et al., 1999; Wimmer and Whitehead, 2004). The different cetacean species that occur within the Gully thus use different habitats within the canyon (Hooker et al., 1999). This is likely to be driven by how oceanographic processes occurring within the canyon influence the distribution of prey for these various cetacean species.

Flow patterns that occur within the Gully are complex and not completely understood, though there is some evidence that enrichment (internal waves, up-canyon flow, upwelling), concentrating (down-canyon flow, downwelling, topographic blockage) and aggregating processes (such as increased habitat diversity and shelter) are all likely to be occurring to some degree within the Gully. The diurnal tide is dramatically amplified by the Gully (Greenan et al., 2014; Swart et al., 2011) and enhanced internal waves that occur in the canyon result in strong vertical mixing that likely increase nutrient levels and primary productivity within the canyon (Petrie et al., 1998; Sandstrom and Elliot, 2002). Mixing in the Gully is approximately 20 times that of the adjacent shelf (Greenan et al., 2014). The observed mixing caused by internal waves within the Gully is among the highest levels of mixing observed anywhere on the Scotian Shelf (Rutherford and Breeze, 2002). However, nutrient levels and phytoplankton abundance in the Gully do not appear to be substantially different from adjacent shelf waters (Head and Harrison, 1998; Yeats and Petrie, 1998), thus it is not clear if such enrichment processes play an important role in attracting cetaceans to the canyon. It is possible that the nutrient influx caused by vertical mixing is transferred outside the canyon. An inflow of water occurs at the mouth of the Gully (Petrie et al., 1998) and flows up-canyon along the eastern side and onto the shelf, resulting in the onshore transport of shelf-edge flow, which intensifies in the spring (Han et al., 2002). This transport of nutrients through the Gully is thought to make a significant contribution to the nutrient pool on the eastern Scotian Shelf (Yeats and Petrie, 1998). Concentrating processes may be more important than enrichment processes for supporting the abundance and diversity of organisms within the Gully. Large concentrations of krill have been documented within the Gully towards the canyon head, likely as a result of topographic blockage (Head and Harrison, 1998; Sameoto et al., 2002). This could lead to increased baleen whale abundance in the canyon (Fig. 1), particularly during the times of year when krill are most abundant on the shelf. Down-canyon flow along the western side of the Gully creates a current along the bottom of the canyon that likely draws small organisms and other organic material into the Gully from feeder canyons along the western side of the Gully and a large trough just north of the canyon head (Rutherford and Breeze, 2002). Such secondary productivity could support benthic and dermersal organisms and increase the abundance of cetacean prey, attracting both toothed and baleen whales to the canyon throughout the year (Fig. 1). Additionally, the bidirectional flow patterns that occur within the Gully (up-canyon flow along the eastern side of the canyon and down-canyon flow along the western side) create a cyclonic partial gyre over the Gully in summer, fall and winter which may retain small particles and weakly swimming organisms within the canyon (Han et al., 2002; Petrie et al., 1998; Rutherford and Breeze, 2002). This retention zone could also increase the abundance of cetacean prey and attract toothed and baleen whales to the canyon throughout the year.

Despite the large body of information that exists on the oceanographic processes and wildlife that occur within the Gully, there is a general lack of knowledge on how exactly these oceanographic processes lead to increased prey density. Future studies should focus on increasing our understanding of the link between the oceanographic processes that occur in the Gully and prey abundance, as well as the distribution and abundance of prey species within the canyon, such as *Gonatus* squid.

5. Conclusions

There are challenges to studying cetacean associations with submarine canyons that need to be addressed in order to gain a more complete understanding of which canyons attract cetaceans and why. Some of the challenges are a result of limited data available on submarine canyons in general, and specifically on the distribution and abundance of cetaceans and their prey in and around submarine canyons. This lack of data is the result of the logistical difficulties of conducting studies in and around these often remote features. As noted above, this means that our understanding of canyon circulation patterns, cetacean distribution and abundance around canyons, and the possible mechanisms that may attract cetaceans, are biased towards the results from a few well-studied canyons. Furthermore, most of the studies reviewed occurred in canyons with known high cetacean abundance, making it difficult to draw general conclusions about cetaceans′ affinity for submarine canyons. In other words, the apparent high degree of association between cetaceans and canyons may simply be an artifact of only studying cetacean distributions in canyons where cetaceans are known to be readily found. As well, while squid have been directly observed in some canyons (*e.g.*, Cailliet et al., 1979; Major, 1968), very little information about squid distribution and abundance around these features is currently available. Deep-water squid species are the primary prey of the cetacean species most commonly observed near submarine canyons on a year-round basis (such as beaked and sperm whales), thus the lack of data on squid in these areas presents a major knowledge gap.

The effects of spatial and temporal scales on the observed distribution patterns of cetaceans within and around submarine canyons also need to be considered. Upper-trophic level marine predators associate with specific physical and biological processes at distinct spatial and temporal scales (Croll et al., 1998; Jaquet, 1996; Jaquet and Whitehead, 1996; Yen et al., 2004). Ecological mechanisms affecting cetacean distribution in submarine canyons may be scale-specific, and there may be a hierarchy of mechanisms operating on varying scales that influence cetacean abundance. It is possible that the effect that a canyon has on prey densities is carried out of the canyon habitat and is actually most pronounced down-stream of the canyon; therefore, data from small-scale surveys centered over canyons may not incorporate enough area to detect the influence of the canyons on cetacean distribution. Small-scale features such as seafloor slope and canyon bathymetry are likely to be important to the success of localized foraging

whales, but data from large-scale surveys may not be useful for predicting cetacean distribution within smaller-scale local habitats (Hamazaki, 2002), such as within canyons. Furthermore, while canyons are static bathymetric features that do not change significantly over short periods of time, the distribution of marine predators and prey may vary seasonally and inter-annually with circulation patterns. Small-scale patches of high prey density are likely to be temporally dynamic over canyons (Ferguson et al., 2006; Genin, 2004) and assessing species distributions in relation to both bathymetry and seasonal circulation patterns is important to gain a more complete understanding of the mechanisms that attract cetaceans to canyons (Yen et al., 2004).

Despite these challenges, evidence of strong cetacean associations with some submarine canyons does exist. Increased cetacean diversity and abundance occur in canyons through a variety of mechanisms that enrich, concentrate and/or aggregate prey. These processes may be permanent features within the canyon occurring on a year-round basis, or may be short-term and seasonal. From the examples of cetacean associations with submarine canyons reviewed, there is some limited evidence that cetaceans may be more likely to associate with larger canyons, though this relationship is not clear. In general, baleen whales occur in canyons only seasonally and are most likely attracted to these features by enrichment and concentrating processes. Concentrating and aggregating processes are more likely to attract toothed whales, which tend to occur within canyons throughout the year. Toothed whales appear to have the strongest associations with submarine canyons, and the cetaceans that most often associate with canyons (beaked whales and sperm whales) feed primarily on squid. It is possible that canyons may be important habitat for squid or somehow make squid more accessible to the whales. Studies of squid populations within and around submarine canyons are needed to determine if squid abundance increases within canyons.

Highlighting the importance of physical features like submarine canyons to cetaceans is of practical importance for management purposes. Environmental variables such as sea surface temperature, chlorophyll levels, salinity and fronts have been used to characterize cetacean distributions (Benson et al., 2002). These are fluid features that change quickly over short time scales and it can be very difficult to establish and enforce boundaries around these moving features to protect cetacean populations from human activities. Physical features of the ocean; however, generally stay fixed over time and can therefore be more easily protected (Hyrenbach et al., 2000).

A more detailed analysis of the physical characteristics and oceanographic processes occurring in canyons known for high cetacean abundance, and comparison to the physical characteristics and oceanographic processes occurring canyons which do not appear to attract cetaceans, would further our understanding of why cetaceans associate with some canyons and not others. Increasing our understanding of the mechanisms that attract cetaceans to submarine canyons may help predict canyon habitats that should be targeted for conservation purposes, as some submarine canyons can indeed be classified as cetacean hotspots and should be protected.

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