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Ecosystem consideration in conservation planning: energy demand of foraging bottlenose whales (*Hyperoodon ampullatus*) in a marine protected area

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Abstract

The Gully, a submarine canyon off eastern Canada, was nominated as a pilot Marine Protected Area (MPA) in 1998, largely to safeguard the vulnerable population of northern bottlenose whales (*Hyperoodon ampullatus*) found there. The boundaries and ultimate management regime for the MPA for this area remain under review. We have estimated the energy consumption of bottlenose whales in the Gully based on the number of whales present at any time, their trophic level, the food requirements of each whale, and the rates of energy transfer between trophic levels. These calculations suggest that there must be a substantial spatial subsidy in the underlying foodweb of the submarine canyon to support the bottlenose whales using the Gully. A substantial area beyond the distribution of bottlenose whales in the area will therefore require protection. Conservation priorities to protect such subsidies will primarily involve additional protection at the level of the sea floor. Spatial subsidies are probably common in the marine environment, urging careful ecological analysis in the establishment of marine reserves and suggesting that conservation priorities need to take into account key ecological linkages and processes that are vital for sustaining species and habitats of concern. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Ecosystem; Marine protected area; Northern bottlenose whale; Spatial subsidy; Submarine canyon

1. Introduction

In December 1998, the Canadian Department of Fisheries and Oceans (DFO) declared the Gully, a submarine canyon off the east coast of Canada, to be a "Pilot Marine Protected Area". This designation was largely based on the residency, small population size ($\sim$130 individuals, Gowans et al., 2000) and vulnerable status (Whitehead et al., 1997a) of the northern bottlenose whales (*Hyperoodon ampullatus*) found there. Five pilot MPAs were designated in Canada as part of the DFO Marine Protected Areas program. The intention is that these areas will be used as models, such that the development of their conservation plans will facilitate the evolution of a national process for establishing MPAs (Fenton et al., 2001). However, despite the intention to provide early protection and management, the process of finalizing the MPA status for these areas is relatively slow.

For effective conservation policy it is widely recognized that an ecosystem-level approach is more effective than that at species-level (Agardy, 1994; Jones, 1994). Theoretically, an ecosystem should encompass all the linkages between species within a defined habitat, but, particularly in the ocean, the spatial boundaries of an ecosystem are often nebulous. Here, we calculate the energetic requirements of top level predators in the Gully, and use this to infer the probable ecosystem structure. The identification and consideration of missing links in this energetic model highlights additional conservation priorities for the area. We suggest that such an ecosystem approach, involving a thorough assessment of the nature and scale of the trophic interactions involved in any marine conservation area is needed for rigorous conservation planning.

Northern bottlenose whales are consistently found in a small area (ca. 200 km^2) above the Gully (Fig. 1; Whitehead et al., 1997a; Hooker et al., 1999). Despite

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search effort in surrounding shelf edge regions, no whales have been observed outside the central canyon area (Fig. 1; Hooker, 1999). This region therefore appears to represent a distributional hotspot for these whales. While in the Gully, bottlenose whales perform regular, very deep dives (to over 800 m depth), apparently in order to forage near the sea floor (Hooker and Baird, 1999). This, together with these whales' preference for deep-water canyon features and the small-scale nature of their movements (Hooker et al., 2001a), the frequency and nature of their sound production in the Gully (Hooker and Whitehead, 2002), and their presence year-round in the area (Whitehead et al., 1997a) suggests that these whales primarily use the Gully area for foraging. However, social activities also appear to take place, as demonstrated by affiliations within groups of whales, the occasional large group sizes observed, and the presence of small calves (Gowans et al., 2001), and these will also require consideration in the establishment of management procedures.

The stomach contents of bottlenose whales from various locations in the north Atlantic show their diet to consist primarily of squid of the genus *Gonatus* (Benjaminsen and Christensen, 1979; Clarke and Kristensen, 1980; Lick and Piatkowski, 1998; Hooker et al., 2001b). Fatty acid and stable isotope analysis of biopsy samples taken from whales in the Gully were consistent with this conclusion, and provided some support for predation on this or similar species (Hooker et al., 2001b). Adult *Gonatus* are found near the sea floor of continental shelves (Kristensen, 1981, 1983), and, as such, their vertical distribution is consistent with the dive records (with regular dives to depths of 800–1450 m) obtained from bottlenose whales (Hooker and Baird, 1999). Arkhipkin and Bjørke (1999) documented the ontogenetic changes in *Gonatus fabricii*, in which the tissues of the females break down as they reach maturity, presumably as an adaptation for deepwater bathypelagic brooding of the negatively buoyant egg masses. They suggested that these brooding females are likely targetted by marine mammal predators. *Gonatus* specimens have been recorded from nearby areas off the Scotian Slope (Dawe and Stephen, 1988), but their abundance and behaviour in the Gully are essentially unknown. Consideration of the energy content of *Gonatus* allows us to estimate the approximate quantity of this squid consumed in the Gully.

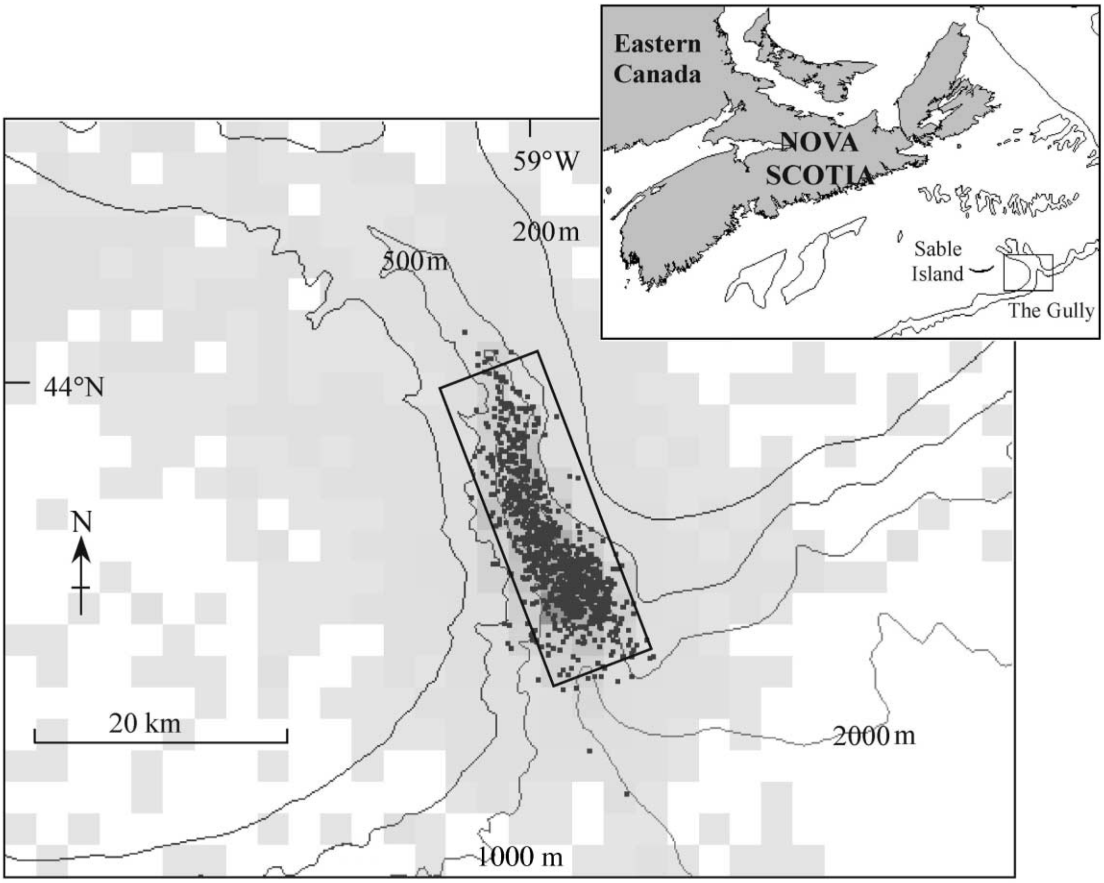

Fig. 1. Map showing location of the Gully submarine canyon (reproduced from Hooker et al., 2001a). Distribution of search effort is illustrated in grey shading for areas spanning 2.5×2.5 km. Square symbols represent northern bottlenose whale sighting locations; 200, 500, 1000 and 2000 m bathymetry contours are shown. Box delineating 8×25 km area (referred to in text) in which almost all bottlenose whale sightings have been observed is shown.

Based on photo-identification records of individual whales, ca. 40 whales are found in the Gully at any one time (Gowans et al., 2000). Individual whales appear to reside in the Gully for ca. 20 days at a time, and there is a continual flux of individuals moving in and out of the area (Gowans et al., 2000). Here we investigate the energetic demands of these whales in the Gully area, particularly in regard to ecosystem structure. Using calculations based on the number of whales in the Gully, assumptions regarding their metabolic requirements and generally accepted trophic models, we estimate the primary productivity required to support these whales. From this, we make recommendations as to the size and nature of the marine protected area that will be required to protect the structure and function of this ecosystem in the Gully.

2. Estimation of energetic requirements

Given a mean length of ca. 6.5 m for a bottlenose whale in the Gully (Whitehead et al., 1997b) and the predicted length–weight equation of $W\ (\mathrm{kg}) = 0.0000131 \times L^{3.07}$ (cm) calculated by Bloch et al. (1996), the mean weight of a bottlenose whale in the Gully would be 5500 kg. Further, given the relationship between basal metabolic rate (BMR) and body weight (W, in kg), $\mathrm{BMR} = 70\ W^{0.75}$ (following Kleiber, 1961), the basal metabolic rate of a bottlenose whale is estimated to be ca. 45,000 kcal/day. In order to calculate consumption rate, BMR must be scaled for a variety of factors such as assimilation efficiency and active metabolism. Following Kenney et al. (1997) we have used a correction factor of 2.5, which leads to a consumption rate of ca. 110,000 kcal/day.

3. Consumption of squid

An adult *Gonatus* has a body composition of ca. 8% lipid (Hooker et al., 2001b) and can be assumed to contain 20% protein (as is common for squid; S.J. Iverson, personal communication). Using energetic conversions of 39.3 kJ/g for fat and 23.6 kJ/g for protein (Blaxter, 1989), the energetic content of adult *Gonatus* is 7.8 kJ/g. The energetic content of a small (18.16 g) specimen of *Gonatus steenstrupi* was measured as 3.78 kJ/g (Clarke et al., 1985). This is probably an underestimate of the calorific value of adults, which have a greater lipid content (Clarke et al., 1985). Assuming the energetic content calculated above (7.8 kJ/g), the mean adult squid (weight 190 g, Arkhipkin and Bjorke, 1999) would therefore provide 1500 kJ, or 360 kcal (1 cal = 4.184 J).

The bottlenose whale consumption of 110,000 kcal/day (calculated above) would therefore be obtained from ca. 300 squid per day. When viewed in conjunction with results from time depth recorders attached to the whales, which show foraging dives approximately every 80 min (Hooker and Baird, 1999), the number of squid an average bottlenose whale would need to eat per dive is in the order of 15–20 squid. The dive records did not show multiple changes in depth and velocity which might be expected from individual chases, suggesting that prey capture may consist of multiple individuals at one time. Consistent with this, Arkhipkin and Bjørke (1999) have suggested that cetacean predators are more likely to feed on the non-motile spawning female life history stage of *Gonatus*.

Since 40 whales (approximately one third of the population) appear to use the Gully at any one time (Gowans et al., 2000), the daily consumption of squid by bottlenose whales in the Gully would therefore amount to 12,000 squid. Although *Gonatus* abundance in the Gully is unknown, the genus is believed to be one of the most abundant nektonic organisms in the North Atlantic (Kristensen, 1984). Bjørke and Gjøsæter (1998) modelled the biomass production of *Gonatus* in the Norwegian Sea (ca. 1.5×10^6 km^2), and suggested that a single cohort of *Gonatus* produces a total biomass of 20 million tonnes.

4. Trophic energetics and level of primary productivity required

Irrespective of the actual prey composition of bottlenose whales, by using the estimated number of whales present in the Gully (40 individuals, Gowans et al., 2000), and their calculated trophic level (Hooker et al., 2001b), we can investigate the potential of the Gully to support this number of whales by calculating the required level of primary production. The nitrogen stable isotope ratio (N^{15}/N^{14}) of bottlenose whales in the Gully was analyzed from skin biopsies. Isotopic nitrogen undergoes a stepwise enrichment of ca. 3‰ at each trophic level, thus providing a useful trophic level marker by which to assess ecosystem structure (Michener and Schell, 1994). The stable isotope ratio of bottlenose whales in the Gully was found to be 15.25‰ δN^{15} (S.E. 0.08‰; Hooker et al., 2001b). Assuming that primary productivity is at ca. 5‰ (trophic level 1; Fry, 1988), with 3‰ enrichment at each trophic level (Michener and Schell, 1994), bottlenose whales occupy a trophic level of about 4.4. This is consistent with the potential foodchain (Fig. 2): bottlenose whales—adult *Gonatus*—shrimps/mysids/fish/other squid—zooplankton—phytoplankton (note: this is undoubtedly an oversimplification of the system but illustrates that a trophic level of between 4 and 5 appears consistent with general models of oceanic foodchains).

The area used by these whales in the Gully is ca. 25×8 km, i.e. 200 km^2 (Fig. 1). Since an average whale

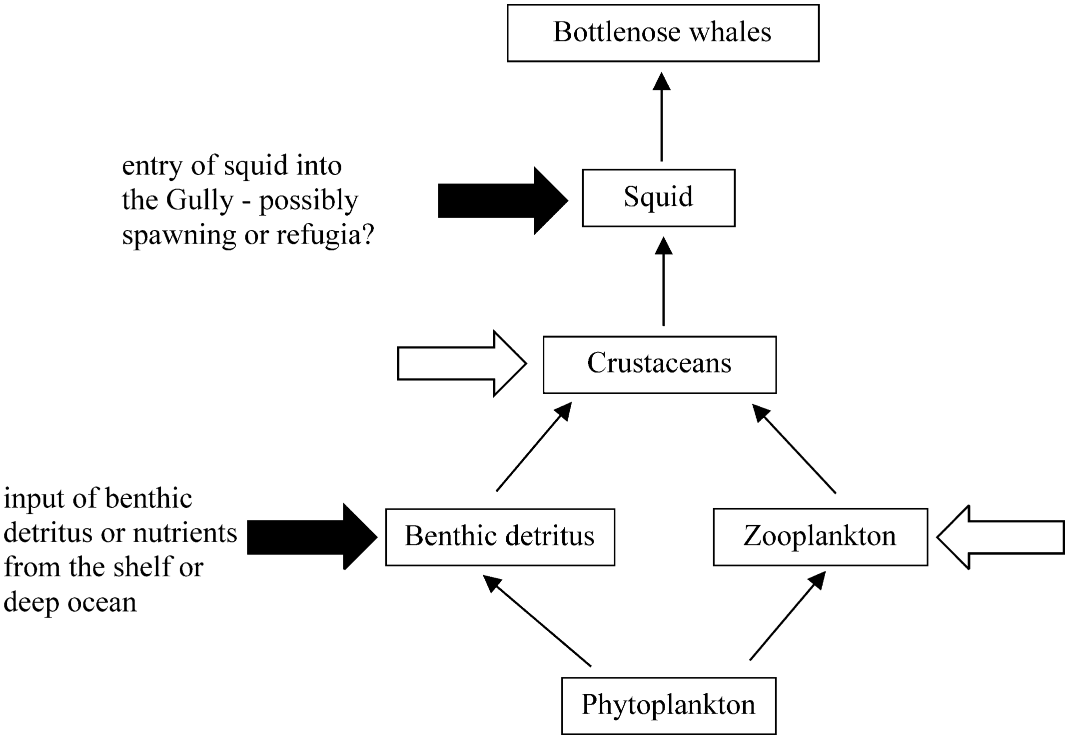

Fig. 2. Diagram of trophic structure of Gully ecosystem showing possible levels of energetic input. Dark arrows show most likely influx (see text for details).

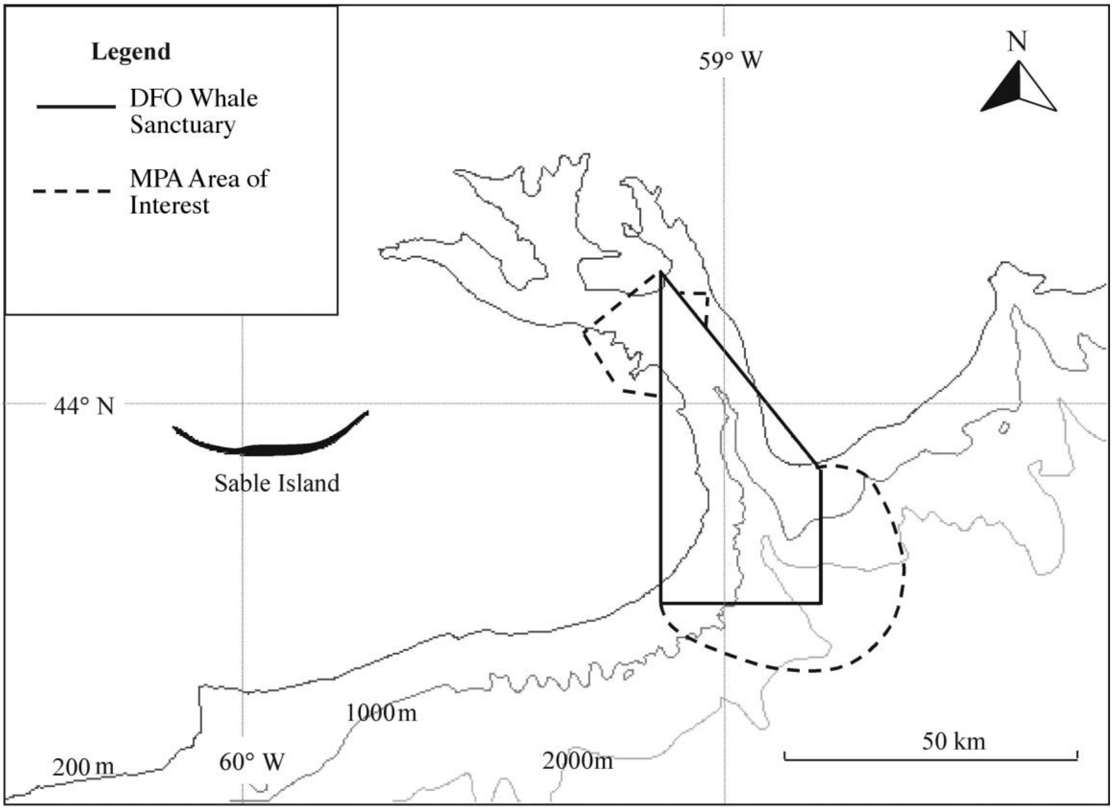

Fig. 3. Boundary of the MPA Area of Interest currently proposed by the Canadian Department of Fisheries and Oceans (based on Fenton et al., 2001).

removes 110,000 kcal per day (calculated above), the total daily energy requirement of 40 bottlenose whales in the Gully is $110{,}000\times40/200\times10^6$ kcal/m^2/day, i.e. 0.022 kcal/m^2/day. Transfer efficiency from one level of the foodchain to the next was assumed to be ca. 10% (Pauly and Christensen, 1995). The primary productivity therefore required to sustain bottlenose whales at this level would therefore be $0.022\times10^{3.4}=55.3$ kcal/m^2/day. Primary production required was converted from energy to carbon by 13.3 kcal/gC (Platt, 1969), resulting in a total required level of primary production of 4.2 gC/m^2/day (1500 gC/m^2/year).

5. Discussion

5.1. Energetic aspects

Estimates of primary productivity range from 0.28 gC/m^2/day (103 gC/m^2/year) in open ocean to 2.7 gC/m^2/day (973 gC/m^2/year) in upwelling systems (Pauly and Christensen, 1995). Overall primary production on the Scotian Shelf was measured at 0.28 gC/m^2/day (102 gC/m^2/year) and that on the Scotian Slope at 0.35 gC/m^2/day (128 gC/m^2/year; Mills and Fournier, 1979). Actual primary production in the Gully does not appear to be anomalously high by comparison with the rest of the Scotian Shelf and shelf break (Harrison and Fenton, 1998). It therefore appears that the level of predation caused by 40 northern bottlenose whales within 200 km^2 (4.2 gC/m^2/day) could not be sustained by primary production in this area. Thus, the Gully must be receiving some form of spatial subsidy from outside of a purely vertical foodchain (c.f. Polis et al., 1997).

An investigation of the assumptions involved in our calculation of required primary productivity supports this conclusion. Other predators were not included in this model, despite the known presence of many other teuthivorous species in this region (Hooker et al., 1999), so the productivity requirements represent the minimum to support the Gully ecosystem (based only on bottlenose whale consumption). The specific prey composition of bottlenose whales has no influence on the calculated energy requirements. These calculations are based only on the estimated trophic level of bottlenose whales, calculated from the stable nitrogen ratio of bottlenose whale skin. Thus the uncertainties that remain over the specific nature of bottlenose whale diet have no impact on these calculations.

In general, the parameters used in the model were chosen to be conservative. For example, the mean body weight of bottlenose whales used here (5500 kg), is derived from a conservative estimate of mean length of bottlenose whales in the Gully of 6.5 m (based on Whitehead et al., 1997b). Similarly, we estimated the area requirements used in the model at 8×25 km area. In fact, this represents the total area in which bottlenose whales have been observed over the 10 years in which they have been studied in the Gully (Fig. 1). In any one year they use a smaller segment of the canyon (Hooker et al., 2001a).

The transfer efficiency of 10% used in this calculation was estimated from 48 fully documented aquatic ecosystems (mean 10.13%, S.E. 0.49; Pauly and Christensen, 1995 and references therein), and so appears to be a fairly robust estimate. However, cephalopods have been recorded with greater transfer efficiencies than this (O'Dor and Wells, 1987), but even assuming their transfer efficiency at 25%, the required primary production would only be reduced to slightly less than half that calculated here. Lastly, although bottlenose whales have been observed in the Gully year-round (Whitehead et al., 1997b), our estimate of the number of whales (40) in the canyon is based on data collected during only three months of the year (June, July, August; Gowans, 1999). It is therefore possible that there might be a reduced abundance of whales during the winter months. However, the lack of any recorded change in whale abundance does not suggest any trend during, immediately prior to, or following the summer months regarding population-level arrival or departure (Hooker, 1999). If there was a reduced abundance during winter, this does not appear to take place until well outside the summer months, leading us to estimate that, at most, this would reduce the yearly energetic requirements by up to a factor of two. Overall, given the likelihood that we have either underestimated required productivity, or only slightly overestimated it, it appears that the Gully ecosystem must be receiving a substantial energetic subsidy to support the bottlenose whales found there.

5.2. Ecology of the Gully canyon

Other aspects of bottlenose whale foraging ecology also suggest that the Gully contains a greater prey abundance for these whales than the surrounding shelf edge areas. The concentrated distribution of whales within the Gully (Fig. 1; Hooker et al., 1999), and the smaller extent of their movements than is generally the case for oceanic species, indicate the presence of a rich and profitable food source, while minor variation in whale use of the area from year to year suggests a relatively stable and dependable system (Hooker et al., 2001a).

The apparent influx of material into the Gully could be occurring at any level within the ecosystem, allowing it to support these whales (Fig. 2). However, a review of the physical and biological oceanography of the region did not reveal much evidence for elevated secondary productivity (i.e. zooplankton) there compared to the rest of the Scotian Shelf (Harrison and Fenton, 1998), so it appears unlikely this influx is occuring at this level.

It has previously been suggested that submarine canyons accumulate organic debris (Vetter, 1994), and it is possible that deep ocean currents (such as the southwestward flowing deep-water in the North Atlantic; Dickson et al., 1990) may bring nutrients or squid prey into the Gully. Unfortunately, little is known about the abundance of prey species of *Gonatus* (thought to be crustaceans and other squid; Kristensen, 1983), but increased levels of sub-surface biomass have not been observed in the region (Hooker, 1999). Harding (1998) has also suggested that the Gully may receive input of benthic detritus from the Scotian Shelf during times of high storm activity. Li et al. (1997) similarly demonstrate the dominance of storm processes in sediment transport on the Scotian Shelf. Lastly, *Gonatus* may grow elsewhere and migrate into the Gully. The Gully has been noted for its deep-sea coral biomass (Breeze and Davis, 1998). One possibility that requires further study is that the Gully may be a spawning location for these squid. Brooding female gonatid squid suffer a degeneration of tissues and loss of tentacles and suckers (Arkhipkin and Bjorke, 1999). These females float at depths of 1000–2000 m with their brooding egg masses, which have been suggested to take up to a year to develop (Okutani et al., 1995; Bjørke et al., 1997; Arkhipkin and Bjorke, 1999; Seibel et al., 2000). It would therefore seem quite likely that spawning gonatid females would seek some kind of refugia for this period, and that the Gully could function as such for these squid.

5.3. The Gully MPA

The Department of Fisheries and Oceans (DFO) is currently in the process of defining the ultimate MPA boundaries and management regime for the Gully area (Fig. 3; Fenton et al., 2001). Currently, the primary boundary for the area is a DFO "whale sanctuary", an advisory area set up in 1994 to minimize the risk of collision with whales, which mariners are recommended to avoid (Fig. 3). DFO is considering an extension of this boundary to include within the Gully Area of Interest (AOI) three small feeder canyons to the west of the Gully and additional area to the south of the Gully (1850 km^2, Fig. 3; Fenton et al., 2001). Such coverage, extending beyond the core area inhabited by bottlenose whales, would satisfy the simple spatial area requirements of our calculations. However, it is more important to establish the nature and location of the spatial subsidy that we have identified. We suggest that this is most likely driven by either the influx of detritus or the influx of squid to the Gully. Therefore, spatially, we would suggest that the areas of the head and mouth of the canyon are most likely to be critical to this process. Although the current AOI protects the mouth waters to the south and the feeder canyons to the west, there may therefore be an ultimate need to extend protection to the area to the north of the Gully, to protect any influx of benthic material in this region.

In terms of management, the primary threats identified for this area include direct threats to the whales (e.g. ship strikes, fisheries entanglements), acoustic impacts (e.g. seismic survey work), or more indirect threats to the ecosystem such as disturbance to substrate (e.g. drilling for oil and gas) and consumptive use of the area (e.g. fisheries). We suggest that the ecological viability of this system is likely to be driven by deep-water or sea floor processes, suggesting that a level of protection is required to minimize disturbance to the sea-floor. Although DFO has not yet established management guidelines for the area, they have requested that no new activities take place within their AOI. Thus the Nova Scotia Petroleum Board is maintaining its policy not to issue calls for Bids in this area, and, in the summer of 1999, the Gully was excluded from the expanding foreign trawl fishery for silver hake (*Merluccius bilinearis*; Fenton et al., 2001). Another major concern associated with this pilot MPA is the impact of sounds into the region, since beaked whales (family Ziphiidae) appear to be particularly susceptible to some high impact sounds (e.g. Simmonds and Lopez-Jurado, 1991; Frantzis, 1998). An effective boundary for seismic survey work was determined during environmental screening for seismic activity on the Scotian Shelf, which recommended a Gully exclusion zone of 10 km from the Whale Sanctuary (Davis et al., 1998). In terms of shipping, although Canada cannot restrict navigation in the exclusive economic zone, Fenton et al. (2001) suggest that new protective designations, such as the International Maritime Organization's Particularly Sensitive Sea Areas, may be worth consideration for the Gully.

Research by the Department of Fisheries and Oceans is ongoing; a recent multidisciplinary research programme has been instigated to attempt to identify the links between the physical environment, productivity questions and cetacean use of the area. Although in practice we laud such attempts to base MPA decisions on a sound understanding of ecosystem structure and function, it seems that sensible and precautionary boundaries can be usefully established based on information currently available.

In conclusion, although ecologists are aware that spatial subsidies are often dramatic in scale and may be variable in nature (Polis et al., 1997), this concept is rarely considered in marine conservation efforts. It has been widely noted that the establishment of marine reserves should be based on ecosystem considerations, but the analysis of foodweb dynamics and their spatio-temporal linkages has been largely ignored. We suggest that, despite the inherent difficulties in assessment of these ecosystem dynamics, their consideration can highlight conservation priorities.

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References

Agardy, M.T., 1994. Advances in marine conservation: the role of marine protected areas. Trends in Ecology and Evolution 9, 267–270.

Arkhipkin, A.I., Bjorke, H., 1999. Ontogenetic changes in morphometric and reproductive indices of the squid *Gonatus fabricii* (Oegopsida, Gonatidae) in the Norwegian Sea. Polar Biology 22, 357–365.

Benjaminsen, T., Christensen, I., 1979. The natural history of the bottlenose whale, *Hyperoodon ampullatus*. In: Winn, H.E., Olla, B.L. (Eds.), Behaviour of Marine Animals: Current Perspectives in Research. Plenum Press, New York, pp. 143–164.

Blaxter, K., 1989. Energy Metabolism in Animals and Man. Cambridge University Press, Cambridge.

Bjørke, H., Gjøsæter, H., 1998. Who eats the larger *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea? ICES CM/M, 10.

Bjørke, H., Hansen, K., Sundt, R.C., 149-. Egg masses of the squid *Gonatus fabricii* (Cephalopoda, Gonatidae) caught with pelagic trawl off northern Norway. SARSIA 82.

Bloch, D., Desportes, G., Zachariassen, M., Christensen, I., 1996. The northern bottlenose whale in the Faroe Islands, 1584–1993. Journal of Zoology, London 239, 123–140.

Breeze, H., Davis, D.S., 1998. Deep sea corals. In: Harrison, W.G., Fenton, D.G. (Eds.), The Gully: A Scientific Review of its Environment and Ecosystem. Department of Fisheries and Oceans, Canadian Stock Assessment Secretariat Research Document 98/83, pp. 113–120.

Clarke, A., Clarke, M.R., Holmes, L.J., Waters, T.D., 1985. Calorific values and elemental analysis of eleven species of oceanic squids (Mollusca: Cephalopoda). Journal of the Marine Biological Association of the UK 65, 983–986.

Clarke, M.R., Kristensen, T.K., 1980. Cephalopod beaks from the stomachs of two northern bottlenosed whales (*Hyperoodon ampullatus*). Journal of the Marine Biological Association of the UK 60, 151–156.

Dawe, E.G., Stephen, S.J., 1988. The cephalopod assemblage of the Gulf Stream system east of 60 W. Malacologia 29, 235–245.

Davis, R.A., Thomson, D.H., Malme, C.I., 1998. Environmental Assessment of Seismic Exploration on the Scotian Shelf (TA 2205. Report by LGL Ltd., King City, ON, for Mobil Oil Properties Ltd., Shell Canada Ltd., Imperial Oil Ltd., and Canada/Nova Scotia Offshore Petroleum Board, Halifax, NS).

Dickson, R.R., Gmitrowicz, E.M., Watson, A.J., 1990. Deep-water renewal in the northern North Atlantic. Nature 344, 848–850.

Fenton, D.G., Macnab, P.A., Rutherford, R.J., 2001. The Sable Gully marine protected area initiative: history and current efforts. In: Proceedings of the Fourth International Conference on Science and Management of Protected Areas, May 14–19 2000, University of Waterloo. SAMPAA, Wolfville, Canada (in press).

Frantzis, A., 1998. Does acoustic testing strand whales? Nature 392, 29.

Fry, B., 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography 33, 1182–1190.

Gowans, S., 1999. Social organization and population structure of northern bottlenose whales in the Gully. PhD dissertation, Dalhousie University, Halifax.

Gowans, S., Whitehead, H., Arch, J.K., Hooker, S.K., 2000. Population size and residency patterns of northern bottlenose whales (*Hyperoodon ampullatus*) using the Gully, Nova Scotia. Journal of Cetacean Research and Management 2, 201–210.

Gowans, S., Whitehead, H., Hooker, S.K., 2001. Social organization in northern bottlenose whales (*Hyperoodon ampullatus*): not driven by deep-water foraging? Animal Behaviour 62, 369–377.

Harding, G., 1998. Submarine canyons: deposition centres for detrital organic matter? In: Harrison, W.G., Fenton, D.G. (Eds.), The Gully: A Scientific Review of its Environment and Ecosystem. Department of Fisheries and Oceans, Canadian Stock Assessment Secretariat Research Document 98/83, Dartmouth, NS, pp. 105–106.

Harrison, W.G., Fenton, D.G., 1998. The Gully: A Scientific Review of its Environment and Ecosystem. Department of Fisheries and Oceans, Ottawa. Canadian Stock Assessment Secretariat Research Document 98/83.

Hooker, S.K., 1999. Resource and habitat use of northern bottlenose whales in the Gully: ecology, diving and ranging behaviour. PhD dissertation, Dalhousie University, Halifax.

Hooker, S.K., Baird, R.W., 1999. Deep-diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). Proceedings of the Royal Society of London B 266, 671–676.

Hooker, S.K., Whitehead, H., 2002. Click characteristics of northern bottlenose whales (*Hyperoodon ampullatus*). Marine Mammal Science (in press).

Hooker, S.K., Whitehead, H., Gowans, S., 1999. Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. Conservation Biology 13, 592–602.

Hooker, S.K., Whitehead, H., Gowans, S., Baird, R.W., 2001a. Fluctuations in distribution and patterns of individual range use of northern bottlenose whales. Marine Ecology Progress Series (in press).

Hooker, S.K., Iverson, S.J., Ostrom, P., Smith, S.C., 2001b. Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. Canadian Journal of Zoology 79, 1442–1454.

Jones, P.J.S., 1994. A review and analysis of the objectives of marine nature reserves. Ocean & Coastal Management 24, 149–178.

Kenney, R.D., Scott, G.P., Thompson, T.J., Winn, H.E., 1997. Estimates of prey consumption and trophic impacts of cetaceans in the USA northeast continental shelf ecosystem. Journal of Northwest Atlantic Fisheries Science 22, 155–171.

Kleiber, M., 1961. The Fire of Life: An Introduction to Animal Energetics. John Wiley, New York.

Kristensen, T.K., 1981. The genus *Gonatus* Gray, 1849 (Mollusca: Cephalopoda) in the North Atlantic. A revision of the North Atlantic species and description of *Gonatus steenstrupi* n. sp. Steenstrupia 7, 61–99.

Kristensen, T.K., 1983. Gonatus fabricii. In: Boyle, P.R. (Ed.), Cephalopod Life Cycles, Vol. 1: Species Accounts. Academic Press, London, pp. 159–173.

Kristensen, T.K., 1984. Biology of the squid *Gonatus fabricii* (Lichtenstein, 1818) from West Greenland waters. Meddelelser om Gronland, Bioscience 13, 1–20.

Li, M.Z., Amos, C.L., Heffler, D.E., 1997. Boundary layer dynamics and sediment transport under storm and non-storm conditions on the Scotian Shelf. Marine Geology 141, 157–181.

Lick, R., Piatkowski, U., 1998. Stomach contents of a northern bottlenose whale (*Hyperoodon ampullatus*) stranded at Hiddensee, Baltic Sea. Journal of the Marine Biological Association of the UK 78, 643–650.

Michener, R.H., Schell, D.M., 1994. Stable isotope ratios as tracers in marine aquatic food webs. In: Lajtha, K., Michener, R.H. (Eds.), Stable Isotopes in Ecology and Environmental Science. Blackwell Scientific Publications, Oxford, pp. 138–157.

Mills, E.L., Fournier, R.O., 1979. Fish production and the marine ecosystems of the Scotian Shelf, eastern Canada. Marine Biology 54, 101–108.

O'Dor, R.K., Wells, M.J., 1987. Energy and nutrient flow. In: Boyle, P.R. (Ed.), Cephalopod Life Cycles, Vol. II. Academic Press, London, pp. 109–133.

Okutani, T., Nakamura, I., Seki, K., 1995. An unusual egg-brooding behavior of an oceanic squid in the Okhotsk sea. Venus (Japanese Journal of Malacology) 54, 237–239.

Pauly, D., Christensen, V., 1995. Primary production required to sustain global fisheries. Nature 374, 255–257.

Platt, T., 1969. The concept of energy efficiency in primary production. Limnology and Oceanography 14, 653–659.

Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28, 289–316.

Seibel, B.A., Hochberg, F.G., Carlini, D.B., 2000. Life history of *Gonatus onyx* (Cephalopoda: Teuthoidea): deep-sea spawning and post-spawning egg care. Marine Biology 137, 519–526.

Simmonds, M.P., Lopez-Jurado, L.F., 1991. Whales and the military. Nature 351, 448.

Vetter, E.W., 1994. Hotspots of benthic production. Nature 372, 47.

Whitehead, H., Faucher, A., Gowans, S., McCarrey, S., 1997a. Status of the northern bottlenose whale, *Hyperoodon ampullatus*, in the Gully, Nova Scotia. Canadian Field-Naturalist 111, 287–292.

Whitehead, H., Gowans, S., Faucher, A., McCarrey, S.W., 1997b. Population analysis of northern bottlenose whales in the Gully, Nova Scotia. Marine Mammal Science 13, 173–185.