IV. DISCUSSION

The current study shows that Auks and Small Gulls were the most abundant of the seabird species-groups. These high abundance sightings and significant species assemblages suggest that the Gulf of Corryvreckan is habitat to pelagic schooling fish species, because these seabird species significantly feed upon herring and sandeels (Barne *et al.* 1997, Barrett *et al.* 2002, Burger & Simpson 1986, Burger *et al.* 1993, Furness 2002, Vermeer *et al.* 1987, Webb *et al.* 1990).

Further studies would be required to confirm the presence of these prey species (Kinder *et al.* 1983), but the significant abundance of the kittiwakes and auks suggest that these fish are present in sustainable numbers, as past studies have deduced from analysis of seabird diets. Furness (2002) found that kittiwake depend upon sandeels as an important part of their diet. Common guillemots are known to feed on a variety of clupeids (SAST unpublished observations in Webb *et al.* 1990), and in the Norwegian Sea, 'fatty' fish (clupeids and sandeels) are essential dietary components of kittiwake, guillemot, razorbill and puffin (Barrett *et al.*, 2002).

Sandeels (*Ammodytes spp.*) are a pelagic schooling fish, widely distributed in Scottish waters and the Firth of Lorn (Barne *et al.*, 1997). They spend some of their daily lifecycle buried coarse sand substrate (Winslade, 1974), but migrate up to shallow waters to feed on planktonic prey species (Furness 2002, Winslade 2002). The surrounding substrates of the Firth of Lorn are comprised of coarse sand and shingle (Admiralty, 2002). The Corryvreckan is boulder-strewn and coarse sediment, due to the extreme tidal currents (Davies 1999, Barne *et al.* 1997). The effects of tidal currents around promontories and headlands can significantly influence abundance of fish species (Uda and Ishino, 1958) and planktonic prey (Zamon, 2002). With predictability in tidal cycles, planktivorous fish species may migrate to areas of high plankton abundance (Alldredge & Hamner 1980; Bray 1981, Hobson 1986, Shapiro & Genin 1993, Noda *et al.* 1994, Zamon 2000 in Zamon 2002), and maybe indirectly associated with water movements in their search for prey (Barnabé & Barnabé-Quet, 2000). Predators that feed on these planktivorous fish species may exhibit foraging behaviours associated with tidal patterns (e.g. Braume & Gaskin 1982, Safina & Burger 1988, Zamon 2000, 2001 in Zamon 2002).

Black guillemot (*Cepphus grylle*) typically forage near the seabed for benthic fish species e.g. butterfish, sculpins and young gadoids (Barrett *et al.* 2002, Webb *et al.* 1990). The steep-sided channel walls are highly influenced by the strong tidal currents (Davis, 1999), but there is a sublittoral community of floral (e.g. *Laminaria spp.*) and faunal (e.g. hydroids and barnacles) organisms (Picton *et al.* 1982 in Barne *et al.* 1997) that can provide habitat for such prey. This study suggests that black guillemots are constrained to certain foraging areas depending upon tidal direction (Alldredge & Hamner, 1980). However, shags were not significantly associated with tidal direction. They also feed close to the seabed (Cooper 1986 in Webb *et al.* 1990), but are recognised as feeding predominantly on sandeels and clupeids in the mid-water zone (Cramp & Simmons 1977 in Webb *et al.* 1990; Wanless *et al.* 1991).

Shags have an average swimming speed of 1.7-1.9 m/s (Wanless *et al.*, 1991). The Gulf of Corryvreckan can run at up to 4.3 m/s (Barne *et al.*, 1997). Presence of shags was not significantly associated with tidal strength, and shags did show higher observations in the near sectors (e.g. CN, DN, BN etc.). Anecdotal evidence (Elliott, *pers. obs.*) suggested eddies, formed by the headlands, occurred on either tidal direction in these sectors. Therefore, shags could feed at tidal fronts, formed by the headlands, regardless of tidal strength or direction and small fish have been associated with quiet zones produced by the lee of a flood tide (Alldredge & Hamner, 1980).

Tidal flow was seen to have a significant effect on the distribution of seabirds and cetaceans in the Gulf of Corryvreckan. All the species that exhibited significant differences between tidal strengths (auks, black guillemots, gannets and porpoise) are subsurface foraging predators. Auks and black guillemots are pursuit-divers (Hume 2003, Burger & Simpson 1986, Webb *et al.* 1990, Zamon 2003). Gannet are a deep diving seabird that searches for prey for up to 40m above the surface and dives deep to catch its prey (Hume, 2003). Porpoise are a small piscivorous marine mammal that searches for pelagic schooling fish (Raum-Suryan *et al.* 1998, Santos & Pierce 2003). The harbour porpoise feeding is possibly linked to prey concentrations and tide currents (Raum-Suryan *et al.*, 1998), and porpoise are known to feed on sandeels (Santos & Pierce, 2003). Gannet and porpoise were seen to be closely associated in feeding locations (Elliott, *pers. obs.*), and anecdotal evidence (Tony Hill, Appendix F) suggests porpoise are not evident on spring tides. This suggests that strong tidal currents define the physiological limitations of foraging of porpoise, gannets and auks. However, the extreme speeds may also affect the concentrations of prey.

Kittiwakes are known to feed not only on sandeels, but also euphasiids and other zooplankton (Vermeer *et al.* 1987, Barrett *et al.* 2002, Hume 2003), and large gulls (e.g. herring gulls and black-backed gulls) are generalist feeders (Hume 2003, Webb *et al.* 1990). Strong tidal fronts and upwellings can cause large aggregations of zooplankton and fish to be forced to the surface where these surface-seizing predators can feed, without being notably affected by the currents (Elliott *pers. obs.*, Camphuysen & Garthe 2001). It has been suggested that when seabirds are foraging on prey at the water's surface, or when there are strong surface indicators of physical mechanisms; there is a strong small-scale association of seabirds and their prey (Brown 1980, Safina & Burger 1985, 1989, Decker 1995, Goss *et al.* 1997 in Swartzman & Hunt 2000), and small-scale physical events have been shown to cause aggregations of zooplankton within their area of influence (Alldredge & Hamner 1980, Hamner & Hauri 1981, Omori & Hamner 1982, Zavodnik 1987 in St. John & Pond 1992). However, it is well regarded that these tidally generated features are difficult to study (St. John & Pond 1992, Zamon 2001).

The evidence from species-groups significantly associated with tidal direction and strength, and sectors allows the proposition that there is a food web based on activity in the Gulf of Corryvreckan.

Table 11 shows the tidal characteristics of the channel associated with tidal direction.

Table 11. The hydrographic characteristics of each sector during an ebb or flood tide.

EBB (East-going Flow)

	FF	EF	DF	CF	BF	AF
Whirlpools		✓	✓			
Fronts/ Line in Sea	✓	✓	✓	✓	✓	✓
Eddies	✓	✓		✓		
Fast Current				✓		
Upwellings				✓	✓	✓
Whirlpools						
Fronts/ Line in Sea	✓			✓	✓	✓
Eddies	✓	✓		✓	✓	✓
Fast Current	✓	✓	✓		✓	
Upwellings					✓	
	FN	EN	DN	CN	BN	AN

FLOOD (West-going Flow)

	FF	EF	DF	CF	BF	AF
Whirlpools	✓	✓				
Fronts/ Line in Sea	✓	✓	✓	✓	✓	
Eddies	✓	✓		✓	✓	
Fast Current	✓	✓	✓	✓		
Upwellings	✓		✓			✓
Whirlpools						
Fronts/ Line in Sea				✓		
Eddies		✓	✓	✓		
Fast Current	✓		✓	✓	✓	
Upwellings	✓			✓		
	FN	EN	DN	CN	BN	AN

Kittiwake and auks feed on sandeels or herring (Barrett *et al.* 2002, Webb *et al.* 1990). They feed mainly on the east-going tides as shown in this study. Although there is no data on the diet, sandeels and herring are common in the area (Barne *et al.* 1997, Webb *et al.* 1990). Kittiwakes and auks feed together along fronts and the results reflect this, along with personal observations (Elliott). Auks and kittiwakes do feed in mixed species feeding flocks, with auks diving and corralling the sandeels against fronts and kittiwakes feeding from above (Camphuysen & Garthe 2001, Hoffman *et al.* 1981, Grover & Olla 1983 in Irons 1998, Zamon 2003). This is substantiated by the far-sector use by auks and kittiwake, which are associated with fronts on east-going and west-going tides. The significance of kittiwake and auk observations on the slack tide direction, in lieu of personal observations, suggests these species-groups wait for the prey aggregations to occur (Irons 1998,). This could be explained by the relationship of zooplankton concentrations, being caused by tidal currents, and the planktivorous predators that are foraging for them (Hamner & Hauri 1977, Alldredge & Hamner 1980, Gagnon & Lacroix 1983, Vermeer *et al.* 1987, Brown & Gaskin 1988, Wolanski & Hamner 1988 in Irons 1983).

Large gulls exhibit opportunistic behaviour by showing no significant use of sectors or tidal strength, but they do favour slack tide when scavenging might be suitable. Shags show no significant activity by tidal direction or strength, however they do favour the near-sectors, especially those centred on the headland, which may suit their slow-swimming speed and shallow to mid-water foraging range (Wanless *et al.*).

Personal observations of porpoise and gannet suggest mackerel (*Scomber scombrus*) and sandeels are present during weak or slack, east-going tides; as suggested by their significant values. Gannet show similar sector use to kittiwakes and auks, although porpoise showed no significant sector use; which may be as a result of difficulties in spotting these discrete cetaceans (DeNardo *et al.*, 2001). Gannet feed on mackerel (Webb *et al.* 1990, Barrett *et al.* 2002), and mackerel are piscivorous pelagic predators (Miller & Loates, 1997). Sandeels are planktivorous, schooling fish that spend part of the diurnal cycle buried in coarse; a substrate local to the Gulf of Corryvreckan (Davies 1999, Admiralty 2002).

The significance of such a ‘hotspot’ is evident by the location of breeding sites. Colonsay (20 miles to the west) is an important nesting site for kittiwakes and common guillemots (Barne *et al.* 1997). In the Firth of Lorn, there were only 17 registered breeding pairs of kittiwake, 30 breeding pairs of common guillemot and 49 breeding pairs of razorbill. With feeding flocks of greater abundance than these, those present in the Gulf must have travelled from either Colonsay, Islay or west Mull; each of which is over 20 miles away (Webb *et al.* 1990).

There are several authors that suggest the hypothesis that in habitats with tidal rips and jets, the energy flow to piscivorous predators is strongly associated with tidal phase (Uda & Ishino 1958, Brown 1980, Johannes 1981, Wolanski & Hamner 1988, review in Hunt *et al.* 1999, Zamon 2001 in Zamon 2003). Tidal phase in this study did not show any significant effect. This may have been due to the categories definition by the median values of tidal height for three local ports. Tidal strength and direction were significant, which agrees with the suggestions that tide topography interacts with the spatial distribution and behaviour of planktivorous fish (Bray 1981, Hobson 1986, Shapiro & Genin 1993, Noda *et al.* 1994, Zamon 2000 in Zamon 2002) and this would explain why predators feeding on planktivorous prey species might also exhibit strong tidal patterns in their foraging behaviour (e.g. Braume & Gaskin 1982, Safina & Burger 1988, Zamon 2000, 2001 in Zamon 2002). This is defined by the ‘tidal-coupling hypothesis’.

If the true biological structure of the Gulf of Corryvreckan is to be understood, more work must be secured. Accurate seabird and cetacean studies are the natural progression. ‘One man living out of a tent’ must expand to a well-structured team study, into seabird densities with accurate hydrographic data to cross correlate. The extreme tidal nature of the Gulf impairs potential surveys through its waters, but intensive analysis of the surrounding waters could improve the understanding of the basic trophic levels. Analysis could be carried out on neap tides, if the hardware could be secured. This report has unearthed a distinct lack of information on a nationally unique environment; which has ‘luckily’ fallen under the ‘umbrella’ of a marine Special Area of Conservation.