TEMPORAL AND SPATIAL VARIATION IN GROUP SIZE OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) IN THE SHANNON ESTUARY, IRELAND

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ABSTRACT

Bottlenose dolphin group size is known to be determined by food availability, social interactions and predator defence. This paper analyses data gathered over seven years from dolphin tour boats operating in the Shannon Estuary and examines whether there were any temporal or spatial trends in group size of the resident group of bottlenose dolphins in the region. Findings indicate that dolphin group size varied significantly between years (ANOVA, $F = 4.55$, $P = 0.0001$), and increased during the months of July, September and October (ANOVA, $F = 8.921$, $P < 0.0001$). Findings also reveal that group size of dolphins encountered in the middle part of the estuary was greater than the outer or inner estuary (ANOVA, $F = 4.176$, $P < 0.001$). The seasonal change in group size is thought to be primarily caused by dolphins switching to different prey species.

INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) are distributed in temperate and tropical waters around the world. They are a remarkably diverse species with populations commonly found in both coastal and offshore habitats (Shane *et al.* 1986).

Bottlenose dolphins are social animals (Foley *et al.* 2010). Most research on bottlenose dolphins has been completed on coastal resident populations as they are easier to locate and study. Bottlenose dolphin group size varies significantly between areas (See Table 1 for examples). Three main factors have been suggested as influencing dolphin group size: food availability, social interactions and predator defence.

Bottlenose dolphins adapt their foraging strategies depending on the abundance and type of prey available (Hanson and Defran 1993). If the prey species forms large schools, coordinated hunting is observed to be an efficient foraging technique. Dolphins integrate their sensory capabilities to locate dispersed schools of fish, and then surround each school to force the fish into a tight 'bait ball' before finally taking it in turns to feed (Gyrgax 2002). When the prey is not a schooling species, it is more beneficial for the dolphins to hunt solitarily or in small groups to reduce intraspecific competition for the limited number of prey (Bearzi *et al.* 1997).

Group size can also be a result of social interactions, for example many studies have noted that groups with calves, otherwise known as 'nursery groups', are generally larger than those without calves (Gibson *et al.* 2013, Gibson and Mann 2008a, Gibson and Mann 2008b, Kerr *et al.* 2005, Mann *et al.* 2000, Reynolds et al. 2000, Bearzi *et al.* 1997, Wells 1991, Johnson and Norris 1986). 'Nursery groups' are composed of adult females that help a mother look after her calf so that she can spend a greater proportion of time foraging to maintain the increased energy needed for lactation (Johnson and Norris 1986). Large nursery groups may also increase protection of vulnerable calves from predators and provide a better learning environment for juvenile dolphins (Gibson and Mann 2008b).

A larger group size may also be a reaction to the occurrence of predators. Larger groups reduce the probability that each individual will be attacked due to the 'dilution effect' (Constantine *et al.* 2004).

Focused studies are needed to determine the key factor that drives change in bottlenose dolphin group size at a particular location.

The Shannon Estuary is located between County Clare, County Kerry and County Limerick on the west coast of Ireland and is 13km wide when it joins the Atlantic Ocean (Fig. 1). It has a diverse marine environment, which supports the only known resident group of bottlenose dolphins in Ireland (Berrow *et al.* 1996). This dolphin population has been recorded in the Shannon Estuary since at least 1835 and is considered to remain stable between 120 and 140 individuals (Berrow *et al.* 2012). Bottlenose dolphins in the Shannon Estuary are genetically discrete compared to others found in

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Table 1—Some examples of the average group size calculated for resident bottlenose dolphin populations around the world

Location	*Country*	*Average group size*	*Population estimate*	*Reference*
Shannon Estuary	Ireland	8.5	107	Berrow *et al.* 2010
Cardigan Bay	Wales	4.59	50	Bristow *et al.* 2001
Moray Firth	Scotland	4.5	129	Wilson 1995, Wilson *et al.* 1999
Northern Adriatic Sea	Croatia	7.4	106	Bearzi *et al.* 1997
Sado Estuary	Portugal	7.8	24	Augusto *et al.* 2011
Sarasota	USA	7	100	Scott *et al.* 1990
San Luis Pass	USA	10.6	71	Maze-Foley *et al.* 2002
Drowned Cayes	Belize	2.9	122	Kerr *et al.* 2005
Ensenada De La Paz	Mexico	12	60	Acevedo 1991
Moreton Bay	Australia	10.6	*	Corkeron 1997
Richmond and Clarence River	Australia	2 to 4	*	Fury *et al.* 2011
Point Lookout	Australia	16.3	321	Corkeron 1997
Doubtful Sound	New Zealand	17.2	83	Lusseau *et al.* 2003

Irish coastal waters and their genetic diversity is stable, suggesting that the dolphins have resided in the Shannon Estuary for centuries (Mirimin *et al.* 2011).

This resident bottlenose dolphin population is protected under the Irish Wildlife Act (1976) and the Wildlife (Amendment) Act (2000), both of which are enforced by the National Parks and Wildlife Service (Ingram and Rogan 2002). In 2000, the Lower River Shannon was designated as a Special Area of Conservation (SAC), as part of the European Natura 2000 network.

Commercial dolphin-watching in the Shannon Estuary began in 1993 and has grown into a significant tourism industry in County Clare (Berrow 2000). Currently, there are two main commercial tour boats that are licensed to dolphin-watch between April and October, and together the two boats carry out between 300 and 400 trips annually. In order to comply with the Shannon Estuary's status as a SAC, tour boat operators must obtain written annual consent from the relevant government department to dolphin-watch in the estuary. As part of their consent they must provide monitoring data through completion of tour boat datasheets, demonstrate competency in environmental education and abide by a code of conduct.

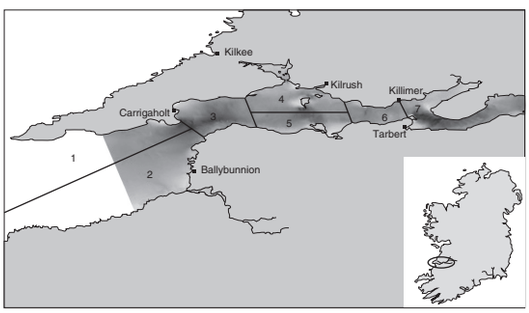

Fig. 1—A map of the Shannon Estuary with the different zones used in spatial analysis. Velocity of current is depicted by shading in the Shannon Estuary, with darker shading representing faster currents. Created on ESRI ArcMap 10.0.

Ingram (2000) found no monthly or seasonal difference in group size, but reported larger group size in the winter than during the summer. In this paper, we used a long term dataset from dolphin tour boats to explore for the first time the biological significance of temporal and spatial change in bottlenose dolphin group size in the Shannon Estuary.

MATERIALS AND METHODS

Datasheets from 2005 to 2011 were collected and analysed from both tour boats (Dolphin Discovery and Draíocht) operating in the Shannon Estuary. In total, 3,376 encounters with dolphin groups were recorded. A datasheet was filled out by both tour boat operators for each dolphin wathcing trip taken over the seven-year period. The datasheet includes information on the length of the trip, the time it took to locate dolphins, the dolphin group size, the number of groups, the number of dolphins and the location of all encounters. The following definition of a 'dolphin group' is used in the datasheet: *all dolphins within a 100m radius of each other or when seen within a period of 5 minutes* (Berrow and O'Brien 2003). A researcher from the Shannon Dolphin and Wildlife Foundation (SDWF) accompanied a dolphin-watching vessel for approximately 10% of trips each year. During those trips, the researcher carried out photo-identification of the dolphins

encountered and completed the same datasheet to that of the tour boat skipper.

There are inherent biases in data collected by tour boat operators. Firstly, tour boats tend to travel mainly on known routes or to where dolphins are more likely to be observed based on previous experience, creating an uneven spatial distribution of trips (Table 2). Secondly, tour boats only operate in good weather conditions and when enough clients have booked a trip; this results in a disproportionate number of trips per month. In addition, although the same recorder (the skipper) completed the datasheets for each trip on *Draíocht* throughout the seven years, different staff recorded dolphin group size each year on *Dolphin Discovery*; this inconsistency may affect the accuracy of data collected.

Statistical analysis was completed using R statistical package software (version 2.14.1, http://cran.r-project.org). To account for the biases described above, a $\log_{10}$ transformation was applied to dolphin group size to normalise data and a combination of ANOVA and t-tests were used to determine whether dolphin group size significantly changed at a temporal or spatial level. All tests were two-tailed: Tukey's Honest Significant Difference (HSD) test was applied to significant results to determine the direction of significance, and the False Discovery Recovery (FDR) correction was used in endpoint adjustment. For the temporal analysis, data from March was excluded due to its very small sample size ($N = 16$). For the spatial analysis, location was given as a number from one to seven depending on which zone of the Shannon Estuary the encounter took place (Fig. 1).

Table 2—Spatial distribution of tour boat effort in the Shannon Estuary. Values show the percentage of trips at each zone for the year. Location codes refer to Figure 1, "DD" = Dolphin Discovery, "DRA" = Draíocht

LOCATION	*1*	*2*	*3*	*4*	*5*	*6*	*7*
2005 DD	1	4	16	9	14	36	21
2006 DD	1	1	16	18	2	30	32
2007 DD	2	1	10	17	9	33	29
2008 DD	0	1	6	17	18	36	22
2009 DD	2	0	25	9	5	26	32
2010 DD	0	1	21	17	19	28	15
2011 DD	4	1	28	5	15	28	20
All years DD	1	1	16	14	12	32	25
2005 DRA	61	16	23	0	0	0	0
2006 DRA	54	20	26	0	0	0	0
2007 DRA	55	25	20	0	0	0	0
2008 DRA	56	17	27	0	0	0	0
2009 DRA	55	23	21	0	0	0	0
2010 DRA	41	23	36	0	0	0	0
2011 DRA	41	18	42	0	0	0	0
All years DRA	52	20	28	0	0	0	0

RESULTS

Average dolphin group size in the Shannon Estuary was 9.71 individuals ($\pm$ 0.12, range = 1–50), but the mean group size recorded from *Draíocht* (10.18 $\pm$ 0.16) was significantly larger than that recorded from *Dolphin Discovery* (8.88 $\pm$ 0.17) (t-test, $t = -3.7905$, $P < 0.001$).

Log_{10} group size was significantly larger in 2005 than other years (ANOVA, $F = 4.55$, $P < 0.001$) when all data was analysed (Fig. 2, Table 3). When data for the two tour boats were analysed separately, only $\log_{10}$ group size from *Dolphin Discovery* was significantly different between the years (ANOVA, $F = 7.022$, $P < 0.001$), with larger $\log_{10}$ group sizes in 2005 and 2006 (Fig. 2, Table 3).

Log_{10} group size varied significantly between months (ANOVA, $F = 8.921$, $P < 0.001$); for *Dolphin Discovery* larger $\log_{10}$ group sizes occurred in September (ANOVA, $F = 3.49$, $P = 0.002$), while larger $\log_{10}$ group sizes occurred in October and July for *Draíocht* (ANOVA, $F = 11.35$, $P = < 0.001$) (Fig. 2, Table 3).

There was also significantly greater $\log_{10}$ group size in zone 3 than any other location when all data was analysed (ANOVA, $F = 4.176$, $P < 0.001$) and when data from *Draíocht* was analysed by itself (ANOCA, $F = 9.106$, $P = < 0.001$) (Fig. 2, Table 3). However, when the location of larger group sizes was compared between years, there was no consistency in the location of the larger group sizes (Fig. 3).

DISCUSSION

The mean dolphin group size of 9.7 individuals is just over the average for resident bottlenose dolphin populations reviewed for this study (Table 1). However, it is nearly double the mean dolphin group size found in other resident bottlenose dolphin populations in the United Kingdom: Moray Firth (4.5) (Wilson 1995) and Cardigan Bay (4.59) (Bristow *et al.* 2001).

The reason for this difference may be a higher abundance of schooling fish species, such as sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), which encourage coordinated hunting techniques (Scott *et al.* 1990). Unfortunately, there is insufficient data on fish assemblage in the Shannon Estuary to test this.

The significant difference in group size over years may be a result of changes in environmental or biological conditions as detailed below, but it may also be due to observer bias. It can be difficult

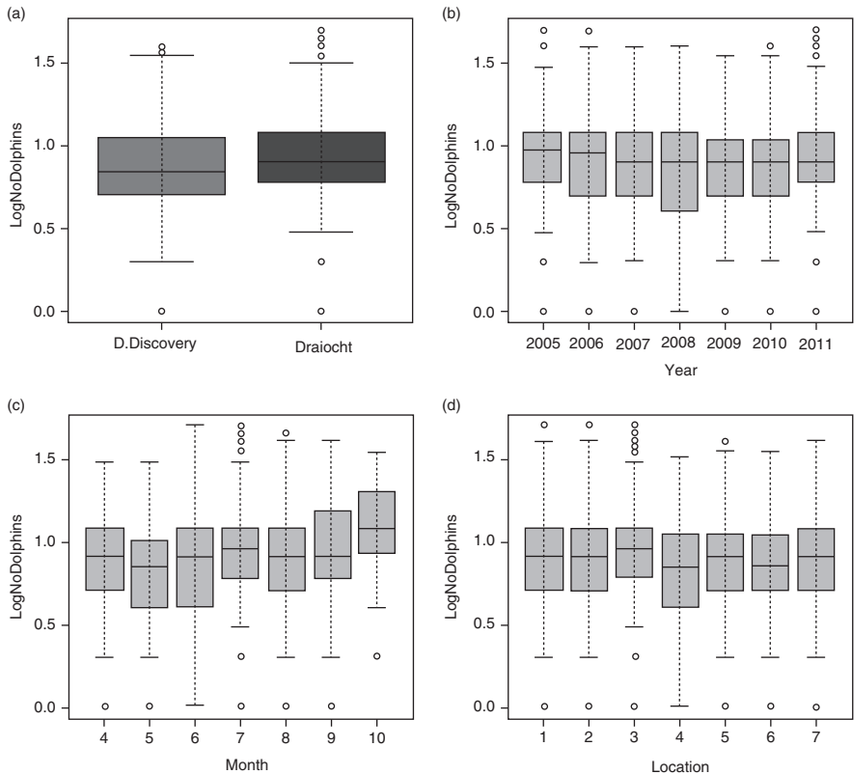

Fig. 2—Comparison of dolphin group size (a) between vessels, (b) between years, (c) between months and (d) between different locations.

for inexperienced observers to accurately estimate bottlenose dolphin group size as dolphins are highly mobile; they move quickly, erratically and often change direction and/or speed while surfacing asynchronously (Wilson et al. 1999). In addition, the sea state, especially in temperate waters, can limit visibility and make it difficult to make accurate counts.

Table 3—Results of statistical tests used to analyse the seasonal and spatial change in dolphin group size

Statistical Test	*Variables tested*	*Test Statistic*	*P*
Significant variables (99% $\alpha = 0.008$)			
t-test	LogNoDolphins (DD) x LogNoDolphins (DRA)	$t = -3.7905$	<0.001
ANOVA	LogNoDolphins x Year [a]	$F = 4.55$ df $= 6$	<0.001
ANOVA	LogNoDolphins (DD) x Year (DD) [b]	$F = 7.022$ df $= 6$	<0.001
ANOVA	LogNoDolphins x Month [c]	$F = 8.921$ df $= 6$	<0.001
ANOVA	LogNoDolphins (DD) x Month (DD) [d]	$F = 3.49$ df $= 6$	0.002
ANOVA	LogNoDolphins (DRA) x Month (DRA) [e]	$F = 11.35$ df $= 6$	<0.001
ANOVA	LogNoDolphins x Location [f]	$F = 4.176$ df $= 6$	<0.001
ANOVA	LogNoDolphins (DRA) x Location (DRA) [g]	$F = 9.106$ df $= 6$	<0.001
Non-significant Variables (99% $\alpha = 0.008$)			
ANOVA	LogNoDolphins (DRA) x Year (DRA)	$F = 2.849$, df $= 6$	0.00913
ANOVA	LogNoDolphins (DD) x Location (DD)	$F = 1.421$, df $= 6$	0.203

LogNoDolphins = number of dolphins recorded with a Log10 transformation
DD = Dolphin Discovery, DRA = Draíocht
Tukey's HSD test results: a = 2005 > 2007, 2009, 2010; b = 2006 > 2008, 2009, 2010 | 2005 > 2008; c = 10 > 4, 5, 6, 7, 8 | 5 < 7, 8, 9 | 7 > 6; d = 9 > 5, 6, 7; e = 10 > 4, 5, 6, 8, 9 | 7 > 4, 5, 6; f = 3 > 4, 6; g = 3 > 1, 2

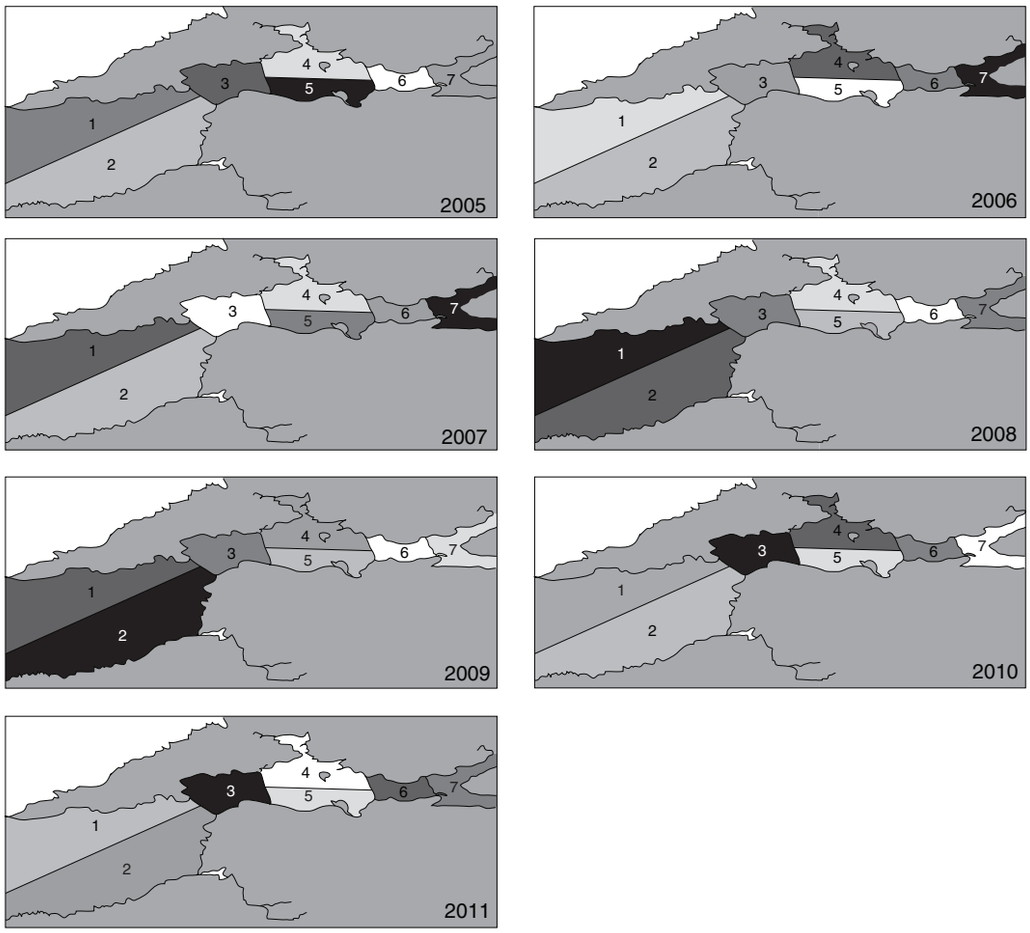

Fig. 3—A plot to show the rank of each zone's mean dolphin group size for each year. Black shading denotes the largest dolphin group size and white denotes the smallest dolphin group size (graduated shading between the largest and smallest group sizes). No zone consistently has the largest groups each year.

In this study, there was significant difference in group size between years recorded by *Dolphin Discovery* but not by *Draíocht*; this may be due to greater variability in *Dolphin Discovery* data collection methods. First, *Dolphin Discovery* used different staff to record dolphin group size each year and thus less-experienced observers may have found it more difficult to estimate dolphin group size. Second, when spatial distribution of tour boat effort was investigated, *Dolphin Discovery* covered all seven zones of the Shannon Estuary and showed greater inter-annual variation in spatial effort than *Draíocht*, which consistently covered just three zones (Table 2, Fig. 1).

Changes in group size as a defence strategy against predators can be ruled out, as there are no known natural predators of bottlenose dolphins in the Shannon Estuary (Berrow *et al.* 1996).

The significantly larger group size observed in September, October and July, compared to other months, may be due to changes in social structure. July is the calving period for bottlenose dolphins in the British Isles (Leatherwood and Reeves 1983). Therefore, the larger group size at this time of year may be the result of the formation of 'nursery groups' (Gibson *et al.* 2013, Kerr *et al.* 2005). Previous research has determined that bottlenose dolphins in the Shannon Estuary calf between June and September, with a peak in August (Ingram 2000). Our data may suggest that the peak could be earlier in the calving period, during July.

The increase in group size in September and October is more likely associated with changes in prey abundance and availability. Bottlenose dolphins show plasticity in their diet and can eat a wide variety of prey, depending on which species are available (Santos *et al.* 2001, Rossbach and Herzing 1999, Defran and Weller 1999, Hanson and Defran 1993). Opportunistic observations of dolphin foraging events have identified dolphins feeding on Atlantic salmon (*Salmo salar*), mackerel (*Scomber scombrus)* and garfish (*Belone belone*) in the Shannon

Estuary (Ingram 2000, SDWF unpublished data). Atlantic salmon return to the estuary to spawn from May onwards (Downes and Gaughran 2012); they are not a schooling species and tend to move upstream in deep channels (Hastie *et al.* 2004). Mackerel move into the estuary from July, while sprat move into the estuary from August to overwinter (ERT (Scotland) Ltd. 2007), and herring migrate into the estuary from September to spawn (Molloy *et al.* 1993). The greater abundance of schooling fish species that appear in the esturary later in the season may attract larger groups of dolphins to feed in a cooperative manner (Würsig 1986).

The observation of larger dolphin group sizes in zone 3 may be attributed to greater concentrations of fish located here. This zone has features known to attract fish, including a deep central channel with steep slopes, high current velocity and tidal eddies (Glass *et al.* 1992; Hastie *et al.* 2004). It also may act as natural 'bottleneck', where the estuary narrows between the headland south of Carrigaholt and the coast north of Ballybunion.

Spatial analysis completed each year over the seven years of the study revealed no consistent trend in where larger groups of dolphins were encountered (Fig. 3). This is most likely an attribute of observer bias; tour boats will only operate in good weather conditions and the timing of these conditions is likely to differ each year. Analysis of the number of tour boat trips for each month revealed that July and August had consistently more trips for both *Dolphin Discovery* and *Draíocht*, but there was a greater level of variation in the number of trips organised in June and September.

Three areas of further research in the Shannon Estuary are recommended to better understand dolphin group size: analysis of the social structure of dolphins in the region could help explain how social interactions affect group size; annual scientific transects across the estuary to identify the location of dolphin groups could be used to better understand the effect of observer bias; and research into the movement of prey species would identify the importance of this in determining group size.

The local fishing fleet in the Shannon Estuary is normally limited to eight small (<15m) fishing vessels catching lobster and crab in pots, and bottom-set tangle nets (Downes and Gaughran 2012). However, in recent years, pair trawlers have occasionally been permitted to catch sprat and herring during the autumn and winter. Between 2003 and 2006, 363 tonnes of herring and 90 tonnes of sprat were landed during 17 days fishing (Department of Marine, *pers. comm.*). Although the catches were relatively small, the removal of ecologically important fish species may impact predator diet. In addition, bottlenose dolphin bycatch in small-scale trawling operations has been identified as a problem in other regions and could also be a threat to dolphins in the Shannon Estuary (Gonzalvo *et al.* 2008, Seco Pon *et al.* 2013, Svane 2005).

The Shannon Estuary is the only SAC for bottlenose dolphins in Ireland, thus the ecological impact of pair trawlers should be fully assessed before fishing commences.

CONCLUSION

This study has identified that bottlenose dolphin group size varies both temporally and spatially in the Shannon Estuary, with food availability suggested as the primary cause of this variation.

When solitary species of fish are more abundant, bottlenose dolphin group size is smaller than when schooling fish species are more abundant. Spatial variation in bottlenose dolphin group size is thought to be primarily caused by the bathymetry or geology of the Shannon Estuary concentrating fish into particular areas.

The influence of different social interactions may also be an important factor in bottlenose dolphin group size, but further behavioural research is required to test this hypothesis.

A precautionary approach to management is recommended in the Shannon Estuary, especially in regards to pair trawling, to ensure that the population of bottlenose dolphins have sufficient food resources available during the autumn and winter months. Although the bottlenose dolphin population have been found in the Shannon Estuary since at least 1835 (Ingram 2000) and have thus survived a number of anthropogenic changes to their environment, they are genetically isolated (Mirimin *et al.* 2011) and any reduction in their population size, no matter how small, could have serious consequences to the population.

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