

The role of synchronized swimming as affiliative and anti-predatory behavior in long-finned pilot whales

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abstract

Synchronized swimming in cetaceans has been hypothesized to play a role in affiliative processes as well as anti-predatory responses. We compared observed variation in synchronized swimming at two research sites in relation to disturbance exposure to test these two hypotheses. This study describes and quantifies pair synchronization in long-finned pilot whales at the Strait of Gibraltar, Spain and Cape Breton, Canada. Synchronization differed depending on the behavioral state and the response is different in the two sites leading to the conclusion that environment can shape the occurrence and magnitude of certain behaviors. We also analyzed intra-population variations in synchronization among 4 social units of Pilot whales in the Strait of Gibraltar and the results of this study confirmed the affiliative role of synchronization and highlighted an influence of disturbance on synchronization. We can conclude that synchronization is a common behavior in long-finned pilot whales that allow for close proximity and rapid coordinated response of individuals, with the multiple functions of showing affiliation and reacting to disturbance.

Keywords:

Synchronization
Strait of Gibraltar
Cape Breton
Long finned pilot whales
GLMM

1. Introduction

Synchronization, as the behavior of several individuals related in time and space, is essential in order to maintain group cohesion in group-living species (Engel and Lamprecht, 1997; Ruckstuhl, 1999). Individuals may appear synchronized because they reacted to the same external stimuli in close proximity (Engel and Lamprecht, 1997). Alternatively, individuals may be synchronized because they modified their behavior to respond to the activity of others. This motor synchronization, defined as “kinesthetic imitation” (Kuczaj and Yeater, 2006), arises when the individual who imitate matches the movements and postures of a demonstrator. It can also emerge from “instinctive imitation” (Morgan, 1990) and “mimicry” (Tomasello, 1999). Such motor synchronization has several fitness advantages. Cooperative feeding and improved foraging, hydro and aerodynamics advantages (Cutts and Speakman, 1994; Weihs, 2004), predation reduction and social facilitation are the commonly highlighted processes responsible for synchronization (Kramer and Graham, 1976; Norris and Schilt, 1987; Gerkema and Verhulst, 1990; Webster and Hurnik, 1994; Whitehead, 1996; Engel and Lamprecht, 1997; Hastie et al., 2003; Fellner et al., 2006; Kuczaj and Yeater, 2006; Tosi and Ferreira, 2008; Patel et al., 2009).

The aim of this study is to assess the role of synchronization in long-finned pilot whales, exploring its role in affiliative and anti-predatory behavior.

Socially facilitated behaviors influence synchronization more than environmental factors (Clayton, 1978; Scott, 1967; Birke, 1974; Webster and Hurnik, 1994). Within a social context, synchronization also promotes cohesion (Birke, 1974; Clayton, 1978) and indicates affiliation (Whitehead, 2008). Cetaceans have the ability to differentiate relationships (on short term and long term basis) and establish higher order alliances as well as cooperative networks. In this context, synchronization appears to facilitate affiliative behavior and to reinforce or advertise social bonds (Connor et al., 2006; Sakai et al., 2009).

Synchronization has also been previously suggested as a response to disturbance (Hamilton, 1971; Collett et al., 1998; Hastie et al., 2003; Hoare et al., 2004; Sumpter, 2006; Carere et al., 2009). In a three dimensional environment, predation risk can be reduced by schooling behavior through an increase in vigilance, “many eyes” effect and a reduction in individual predation risk (Kramer and Graham, 1976; Norris and Schilt, 1987; Gerkema and Verhulst, 1990; Bednekoff and Lima, 1998; Fellner et al., 2006). The rapid exchange of information in a cheating-proof environment (Norris and Schilt, 1987) allows faster reaction, increases surveillance and mediates the confusion of predators. Sensory integrated system (SIS) has been detected in several taxa including fish, birds and cetaceans and permits the school to function as a

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hypersensitive organism (Fellner et al., 2006) enhancing individual vigilance. SIS requires a close spatial distribution and a high degree of synchronization, reducing inter-individual distance and a faster information transfer. Synchronous air breathing of social fishes (Kramer and Graham, 1976), synchronous feeding of common voles (Gerkema and Verhulst, 1990), synchronous behavioral state in bighorn (*Ovis canadensis*) males and ibex groups (Ruckstuhl, 1999; Ruckstuhl and Neuhaus, 2001) and synchronous foraging macaques (*Macaca fuscata yakui*) (Agetsuma, 1995) are all examples of anti-predatory synchronization.

Synchronization has been reported as an anti-predator response in cetaceans to both predators and human (boat) presence (Heimlich-Boran, 1988; Norris and Dohl, 1980; Hastie et al., 2003; Senigaglia and Whitehead, 2011). Norris and Dohl (1980) report how spinner dolphins tend to swim in tighter and more synchronized groups under predation risk. In a similar manner synchronized resting behavior in killer whales and synchronized diving in sperm whales have been linked to enhanced vigilance against predators (Heimlich-Boran, 1988; Whitehead, 1996). Synchronization for social facilitation has also been suggested for cetacean (Mann and Smuts, 1999; Connor et al., 2006;

Senigaglia and Whitehead, 2011). Several studies report the importance of mother calf synchronization during the first months of the calf life (Mann and Smuts, 1999). Moreover synchronization occurs during social interactions and among male alliances in bottlenose dolphin in Shark Bay and it has been linked to affiliation behavior (Connor et al., 2006). We aim in this study to test whether synchronization can indeed be used for both affiliation and anti-predation by comparing synchronized swimming behavior in two genetically different populations of long-finned pilot whales (Verborgh et al., 2010) exposed to different socio-ecological conditions. The two study sites, Cape Breton (Canada) and the Strait of Gibraltar (Spain) have low and high residency pattern of Pilot whales population encountered, respectively and present low and high degree of vessel traffic and anthropogenic disturbance respectively. Hence if synchronization serves as proxy for affiliation then we expect it to vary when chances for social bonding are higher as in case of a resident population. Moreover, if synchronization is used as anti predatory strategy then its occurrence will be higher in a more stressful environment where animals are exposed to higher levels of disturbance.

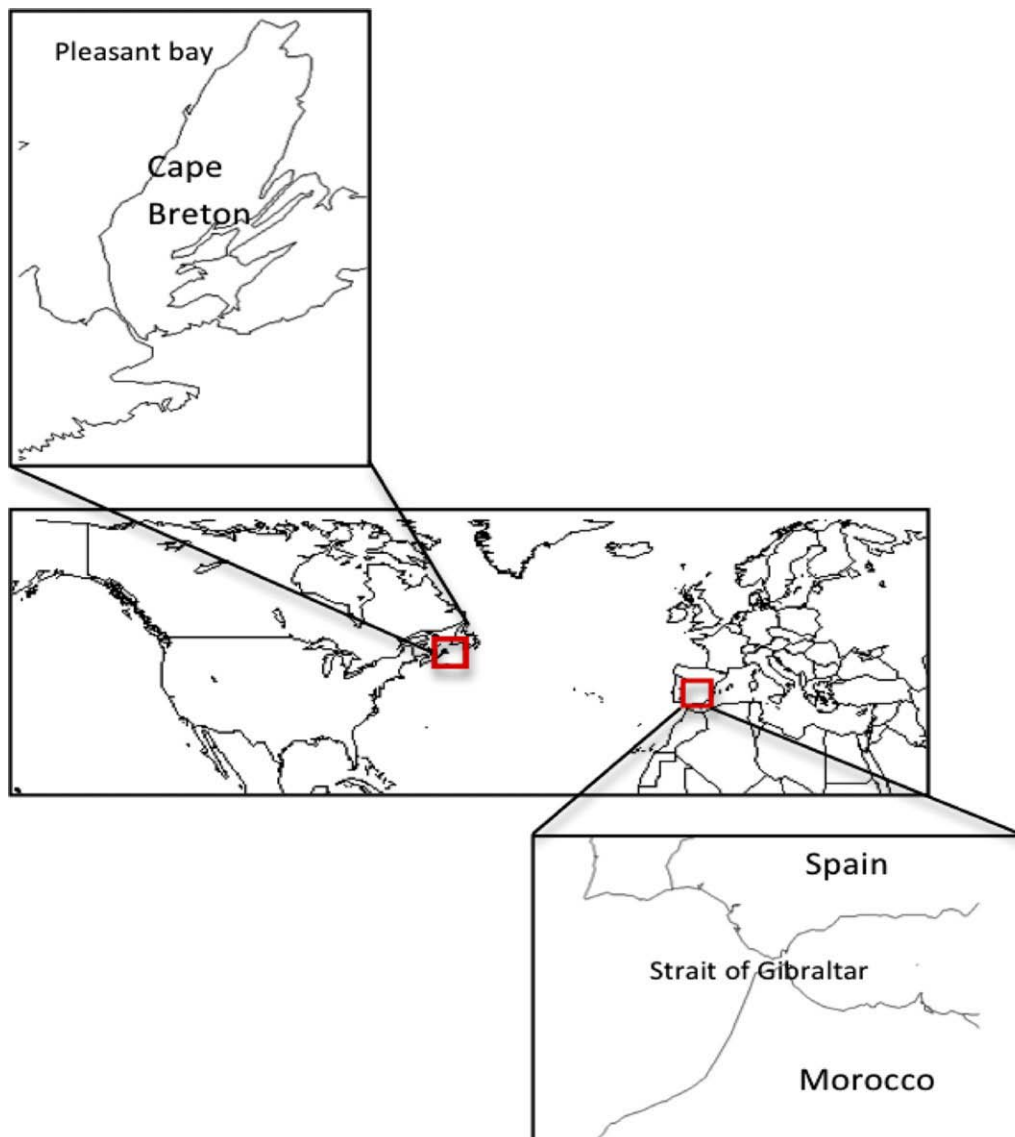


Fig. 1. Map showing the two field sites position in respect of the Northern Hemisphere. Cape Breton, Nova Scotia, Canada on the top left and the Strait of Gibraltar between Spain and Morocco on the bottom right.

2. Methods

2.1. Study areas

Data were collected in Pleasant Bay, in Cape Breton Island situated northwest of Nova Scotia, Canada (46° 50'N, 60° 47'W) (Fig. 1). In this area during the summer over 1000 pilot whales (Ottensmeyer and Whitehead, 2003) converge following the migration of squid, *Illex illecebrosus* (Sergeant, 1962). Between July and August 2008, surveys were conducted on a daily bases, weather permitting, to collect data on distribution and behavior of long-finned pilot whales, from a whale-watching platform. In the Strait of Gibraltar a stable population of 213 pilot whales inhabits this area (Verborgh et al., 2009), sympatric with bottlenose dolphins and sperm whales during the summer months (de Stephanis et al., 2008a). Data on behavior and synchronization in this area have been collected from March to July 2010 from a dedicated platform, Elsa, a 10 m motor boat equipped with an observation post situated at 4 m from sea level.

Behavioral data have been collected in both sites using a similar protocol. Focal group follow protocol was used and data were recorded every 10 min through scan sampling (Mann, 1999). Visual behavioral observations have been aided by videos, documenting the surface behavior of the animals, allowing a greater precision in the descriptions of the various behaviors and the assessment of breathing synchronization. Digital videos of a maximum duration of 2 min were filmed, using a Canon JVC HDD EVERIO, 30 GB Hybrid, with Konica Minolta lens and 35x optical zoom. For further details on data collection see Senigaglia and Whitehead (2011)

2.2. Analysis

2.2.1. Video processing

Video recordings were taken from 157 sightings (69 in Nova Scotia, and 88 in the Strait of Gibraltar). A total of 968 min of video were filmed (138 min for Cape Breton, and 830 for the Strait of Gibraltar), lasting a total of 200 videos for both areas. The videos were filmed and analyzed using the same procedure for both areas. Videos were analyzed frame by frame to measure synchronization, recording every surface of pairs of individuals. Synchronization was measured as paired surfacing and as synchronized breathing. These two measurements allow us to analyze synchronization at two temporal scales to explore the function of this behavior. Paired surfacing was defined as two individuals traveling in the same direction, sharing part of the same surface interval, at a distance equal or less to a body width and with an inter-breathing lag of maximum 3 s, while synchronized breathing was defined as two individuals breathing within 1 s from each other. To establish these pairs in case of multiple individuals corresponding to the previous criteria we used a closest-neighbor approach. The surfaces were then described taking into account the difference, in seconds, between the two whales' breaths (GBT). To compare the time of respiration within the pair, the time of the individual's breath was recorded at the nearest second and a breath start was defined as the first advice of the white foam was visible at the surface (Lafortuna et al., 2003).

2.2.2. Statistical analysis

2.2.2.1. Comparing Cape Breton and the Strait of Gibraltar. Due to the different video length in Cape Breton and Gibraltar (2 min versus ad libitum recordings respectively), we used a Monte Carlo approach to sub-sample the Strait of Gibraltar dataset to achieve samples comparable to the Cape Breton dataset. We took at random two minutes of video for each video sample and then calculated the difference in time between the start of the encounter and the selected two minutes (TBV). We considered the duration of the boat interaction to that point as a proxy of boat disturbance because of the

cumulative stress to which the whales were subjected facing a stalkative predator. The distance and behavior of the boat during all the encounters was considered the same. Within the two minutes the potential disturbance of the boat was considered constant. Only one video was recorded per each encounter and was used as statistical unit. GBT was then transformed into a dummy variable scoring synchronized pairs with breath intervals of 0 and 1 s as synchronized breathing (1) and breathing intervals of 2 and 3 s as not synchronized breathing (0).

2.2.2.2. Anti predation or affiliative behavior. We analyzed the relationship between the dependent variables (number of synchronized pairs and proportion of synchronized breathing) and the explanatory variables using generalized linear models (GLM). We developed biologically relevant contrasting models based on a previous study (Table 1; Senigaglia and Whitehead, 2011). School size (defined as the total number of individuals including calves), behavioral state and TBV were found to be the most meaningful parameters in our previous study hence were used as explanatory variables in our models, adding a site (Strait of Gibraltar versus Cape Breton) effect. If anti-predation was the predominant process influencing synchronization, we would expect models including TBV to best explain the observed variance in synchronization (models 7–9). However, if affiliative behavior was the predominant process influencing synchronization, we would expect models including variation between the two sites and behavioral states to best explain observed synchronization patterns. In fact synchronous movements varies among different behavioral states (Fellner et al., 2006) and affiliative behavior is favored by kinship and long-term relationships (Connor et al., 2006). The occurrence of long lasting association and the animals' behavioral budget could differ if the population is resident or transient within the study area.

2.2.2.3. Paired surfacing. Ten contrasting models were tested to explain the observed variance in the number of paired surfaces within each video (Nsurf) (Table 1) using (GLM) and a "log" link function for count data with Poisson error distribution.

The model selection was performed using Akaike's Information Criteria (AIC), this tool select the best-fitted model based on a maximum likelihood approach, favoring more parsimonious models. The model fit depended on the Monte Carlo sampling we carried out to standardize data across the two sites. In order to determine the sensitivity of results to this approach we ran each model 100 times (obtaining 100 subsamples of the Gibraltar dataset) to obtain a distribution of AIC and the mean value was used in the model selection process. Once the best-fitted model was chosen (Table 2), it was run for 1000 iterations to obtain the mean estimate value

Table 1

Models for large-scale analysis run 100 times to obtain mean AIC values for model comparison. The response variable Nsurf represents the overall number of paired surfaces (dyads of whales surfacing and exhaling within 3 s of each others) within each video. Standard errors (SE) associated with mean AIC values are also provided.

Model	Mean AIC	SE
1. Nsurf~(site × group size)+(site × behavior)	1029.904	2.258
2. Nsurf~ site + group size + behavior	1038.963	2.113
3. Nsurf~ site + group size	1046.761	2.290
4. Nsurf~ group size + behavior	1046.819	2.444
5. Nsurf~ site × group size	1065.662	2.501
6. Nsurf~ group size	1069.102	2.470
7. Nsurf~ site × TBV	1086.413	2.427
8. Nsurf~ site + TBV	1088.319	2.848
9. Nsurf~ TBV	1091.142	2.538
10. Nsurf~ site	1098.928	2.303

Table 2

List of parameters from best fitting model in large-scale analysis. The response variable used was the overall number of paired surfaces per video. Each row represents a parameter of the model and the two columns show the mean parameter coefficient and the number of time in which the parameter was found significant (p -value < 0.05) over 1000 permutations. Standard errors (SE) associated with parameters' coefficient are also provided.

	Mean parameter coefficient	SE	N p-value < 0.05
Site	0.07795	0.004	6
Group size	0.03541	0.0002	999
Resting behavior	0.34388	0.004	392
Socializing behavior	-0.0474	0.005	24
Traveling behavior	0.29708	0.004	166
Site \times group size	-0.02193	0.0002	649
Site \times resting	0.02078	0.004	2
Site \times socializing	0.88943	0.005	960
Site \times traveling	0.30364	0.004	157

and the number of time in which each explanatory variable was found significant (p -value < 0.05).

2.2.2.4. Consistency among social units in the Gibraltar population. Long-finned pilot whales live in long-lasting social units (Amos et al., 1993; de Stephanis et al., 2008b). To test whether individuals behave differently among different social units, we run again the models using only the Gibraltar dataset where the social group could be defined by photo-identification (see de Stephanis et al., 2008b; Verborgh et al., 2009 for details). We added social unit membership as a random effect within a generalized linear mixed effect model (GLMM) framework. The analyses were performed in R using lme4 package (Bates and Maechler, 2010). We restricted analyses to videos containing a single social unit (6 videos from unit C, 12 from unit D, 8 from unit G and 9 from unit F). In addition to paired surfacing we also assessed variation in synchronized breathing. The proportion of synchronized paired surfaces to the overall number of paired surfaces was used as a dependent variable. We used the same Monte Carlo procedure as described in the previous section. The binomial GLMMs were run 100 times to select best fitted one according to AIC and then the selected model was run 1000 times in order to obtain an AIC distribution and percentage of significance of the explanatory variables.

Similar analyses at fine scale were impossible to be conducted for Cape Breton dataset as we were unable to identify social units in the field. However multiple observations of the same individuals may lead to statistical issues for non inter-independence of data. We accounted for this potential bias during the analyses conducted in our first paper (Senigaglia and Whitehead, 2011) by adding "video sequence" as a control variable in our models and analysing just one sequence per encounter. The control variable was not included in the best model so it would have been redundant to add it again in this further analysis.

3. Results

3.1. Paired surfacing

When the overall number of paired surfaces was used as the response variable, the best-fitted model according to the iterated AIC values included site, behavioral state and group size as explanatory variable and also the interaction of site and group size and site and behavioral state. We are confident in the choice of this model based on the difference in AIC values between our best model (AIC = 1029) and the second best (AIC = 1038) that included both behavioral state and group size but ignored their interaction with sites. For more details on each tested model refer to Table 1. Behavioral states influenced the number of observed paired surfacing;

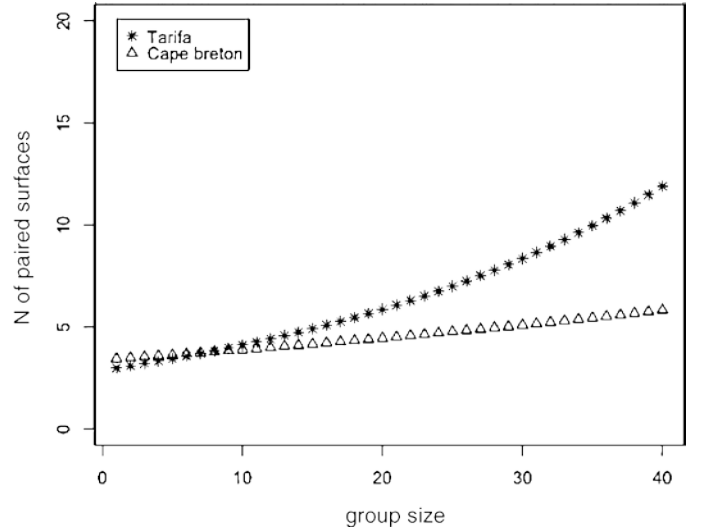


Fig. 2. Effect of group size on the overall number of paired surfaces observed over a 2-min period in Cape Breton and Strait of Gibraltar.

however, the nature of this relation differs according to the site. Synchronization was more likely to be observed during traveling and resting in the Strait of Gibraltar while it was more likely to be observed during socializing in Cape Breton (Fig. 2).

3.2. Within social units analysis

Both TBV and group size were found affecting the overall number of paired surfaces among social units while considering dyad synchronization differences within social units, the best fitting model according to AIC value included only TBV (Table 3).

Interestingly, the overall number of paired surfaces increased with TBV (0.365; SE = 0.02), while the proportion of synchronized breathing decreased with TBV (-0.01 ; SE = 0.001) (Figs. 3–5).

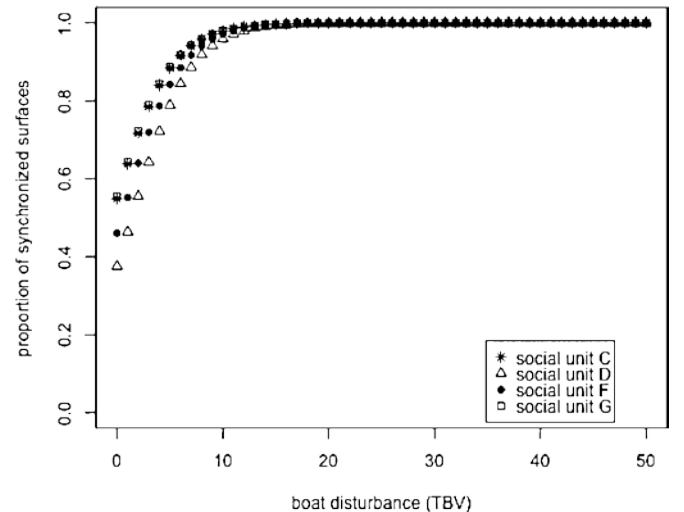


Fig. 3. Relationship between TBV (time elapsed between the start of the encounter and the beginning of the video) and the proportion of synchronization within paired surfaces.

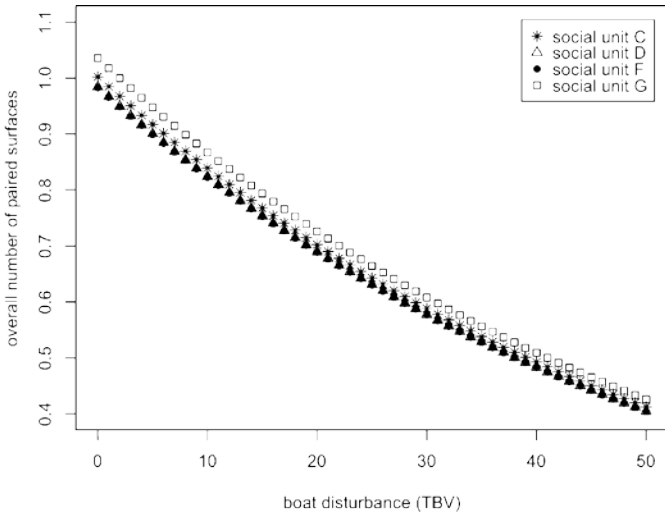


Fig. 4. Relationship between the overall number of paired surfacing and TBV (time elapsed between the start of the encounter and the beginning of the video) per social group in the Strait of Gibraltar. Social groups have been defined in [de Stephanis et al. \(2008b\)](#).

4. Discussion

4.1. Inter-site variation in paired surfacing

The results support synchronization as an affiliative behavioral process in pilot whales. The overall number of paired surfaces occurring within 3 s of each other was influenced by the behavioral state and group size but their effects differed between sites. We hypothesized that synchronization is a component of affiliative behavior hence a likely explanation for the difference in response across the two sites relates to the different composition of the pilot whale aggregations encountered at those two locations. In the Strait of Gibraltar the population is resident year-around ([Verborgh et al., 2009](#)) while in Cape Breton numerous social units converge in the area from the North Atlantic only during summer months to forage and mate ([Ottensmeyer and Whitehead, 2003](#)). In this latter situation individuals from various social units can aggregate in groups by chance or deliberately choosing unrelated social units

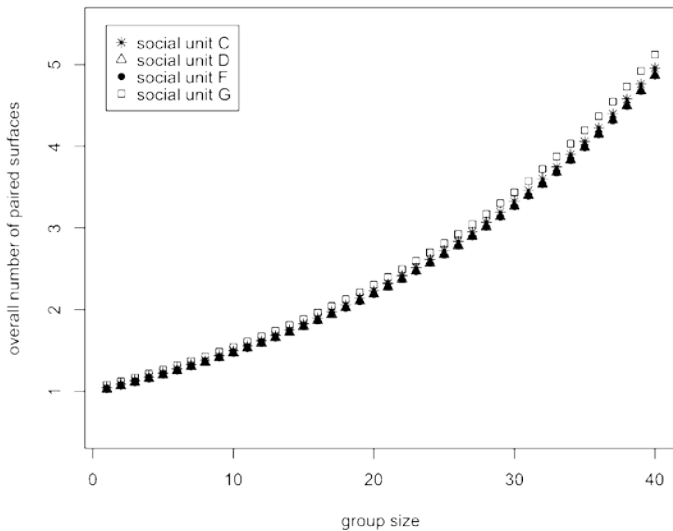


Fig. 5. Relationship between the overall number of paired surfacing and group size per social group in the Strait of Gibraltar. Social groups have been defined in [de Stephanis et al. \(2008b\)](#).

for mating purposes. In contrast, different social units will congregate actively looking for specific favorite companions in the Strait of Gibraltar. [Sakai et al. \(2011\)](#) and [Perelberg and Schuster \(2009\)](#) report higher synchrony degree among dyads of same sex and age and those associations are more likely to occur in long lasting relationship than in casual acquaintances of mating individuals. Sex and age have not been considered in our analysis because no reliable method exists to age and sex pilot whales in the wild ([Ottensmeyer and Whitehead, 2003](#)). However data collection in Cape Breton occurred during mating season and our findings support [Perelberg and Schuster \(2009\)](#) conclusion of a smaller chance to detect synchronization with a higher occurrence of mating pairs. They also suggested that synchronization represents an act of cooperation with delayed gain in terms of increased in fitness due to bond maintenance and social stability. In that case, synchronization should be promoted in a more stable and close population in which the odds to re-encounter individuals are higher. Synchronization implies matching individual activity to group behavior and this could carry a cost for the individual that has to modify its optimal behavioral budget ([Conradt and Roper, 2000](#)). Generally this cost is counterbalanced by the gain of social grouping as decreased predation risk and increased prey capture ([Morrell et al., 2011](#)). However, there is no record of cooperative feeding in long-finned pilot whales. In addition, in Cape Breton, it would be more beneficial for the individuals to closely associate in small social units avoiding inter-units mixing when not necessary, and hence avoiding scramble competition costs. A similar synchronization pattern is found in Fallow deer (*Dama dama*) that present less synchronized movement with increasing group size to reduce foraging interference ([Focardi and Pecchioli, 2005](#)).

4.2. Synchronization within social units

A certain degree of diversity in diet specialization has been reported between social units in the Strait of Gibraltar ([de Stephanis et al., 2008c](#)). The variance in synchronization is better explained considering social units as a random effect. This supports that synchronization is a proxy for imitative behavior and consequent social learning through motor and acoustic imitation ([Rendell and Whitehead, 2001](#)).

Anthropogenic disturbance, expressed as the time spent with the dolphin prior to the occurrence of synchronization, has an effect on both the overall number of paired surfaces and the proportion of synchronized breathing. However, the nature of this effect varies according to the response variable used. The occurrence of paired surfaces decreased as time spent with

Table 3

Models for social units analysis run 100 times to obtain mean AIC values for model comparison. Each row corresponds to a model and each column to a different response variable. The response variable N_{synch} represent the proportion of synchronized surfaces (two individuals breathing maximum 1 s apart) on the overall number of paired surfaces while the variable N_{surf} represents the overall number of paired surfaces (dyads of whales surfacing and exhaling within 3 s of each others) within each video. The cells are then filled with the mean AIC value for the correspondent model. Standard errors (SE) associated with mean AIC values are also provided.

Model	N_{surf}	SE	N_{synch}	SE
1. $\sim \text{TBV} + (1 \text{social-units})$	98.3	3.006	24.26464	0.743
2. $\sim \text{Group size} + (1 \text{social-units})$	98.7	2.960	25.67959	0.745
3. $\sim \text{TBV} + \text{group size} + (1 \text{social-units})$	95.1645	2.905	25.10971	0.778
4. $\sim \text{TBV} \times \text{group size} + (1 \text{social-units})$	95.6798	2.810	26.288	0.827
5. $\sim \text{TBV} + \text{socialUnits}$	194.7306	5.771	28.63269	0.881
6. $\sim \text{Group size} + \text{socialUnits}$	192.0439	5.830	29.15646	0.897
7. $\sim \text{TBV}$	197.7179	5.795	30.0358	0.905
8. $\sim \text{Group size}$	191.14	5.720	30.3062	0.937
9. $\sim \text{Group size} \times \text{socialUnits}$	195.2774	5.856	32.85148	0.973
10. $\sim \text{TBV} \times \text{socialUnits}$	192.8514	5.748	33.86735	1.019

the boat increase while synchronized breathing increased with longer boat interactions (TBV). This suggests multiple functions of synchronization, the prolonged presence of boat may lead to behavioral disruption that can decrease the occurrence of affiliative behaviors and may disperse the group preventing from paired surfaces. At the same time for those dyads that already engage in pair swimming, an increase in the degree of synchronization could be necessary to maintain proximity in a potentially stressful situation as being chased by a boat. Hence, synchronization could also function as anti-predatory response for those dyads in which affiliative relations are well established and the proximity and movement synchronization assume different meaning (e.g. mother-calf pairs or long-term alliances). Influence of TBV on synchronization within dyads confirms our previous findings (Senigaglia and Whitehead, 2011) suggesting a more general function of synchronization as antipredatory response to a perceived risk regardless the intensity of the stimulus.

The limitation of our equipment and the consequent inability of recognize the individuals within the pairs prevented us for following the pairs for multiple dives. Further studies on synchronization aided by recording devices that allow for individual identification may provide further evidence or synchronization as affiliative behavior. Moreover preference association pattern among Pilot whales have been already suggested both in Cape Breton and in the Strait of Gibraltar. Hence a study coupling long term association, kin relationships and synchronization degree may highlight further degree of alliances among individuals. Moreover experimental approach and predator play back experiments may be added to the research protocol in order to support the hypothesis that synchronization may act as an antipredatory strategy.

5. Conclusion

This study provided evidence that synchronized breathing is an important component of pair swimming and has a functional role in affiliative behavior. Influence of behavioral state and group size on synchronization was detected, however their effect differed between populations. The results also suggest an influence of group size and disturbance on synchronization among different social units in the Strait of Gibraltar. Therefore while synchronization could be a general anti-predatory response to a perceived risk, we hypothesize that its importance in maintaining social associations will differ according to the social landscape of the population.

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