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Fish farming and its appeal to common bottlenose dolphins: modelling habitat use in a Mediterranean embayment

SILVIA BONIZZONI[a,b,c,d,*], NATHAN B. FUREY[d,e], ENRICO PIROTTA[c,f], VASILIS D. VALAVANIS[g], BERND WÜRSIG[d] and GIOVANNI BEARZI[a,b,d]
[a]*Dolphin Biology & Conservation, Piegaro PG, Italy*
[b]*OceanCare, CH-8820 Wädenswil, Switzerland*
[c]*Tethys Research Institute, Milan, Italy*
[d]*Texas A&M University at Galveston, Galveston, TX, USA*
[e]*Pacific Salmon Ecology and Conservation Laboratory, Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC, Canada*
[f]*Institute of Biological & Environmental Sciences, University of Aberdeen, Aberdeen, U.K.*
[g]*Marine Geographic Information Systems Lab, Hellenic Center for Marine Research, Iraklion Crete, Greece*

ABSTRACT

1. Common bottlenose dolphins *Tursiops truncatus* interact with fish farms in the Mediterranean Sea. These interactions were investigated in a Greek bay by incorporating multiple geographic, bathymetric, oceanographic, and anthropogenic variables.
2. Generalized additive models (GAMs) and generalized estimation equations (GEEs) were used to describe dolphin presence. Visual surveys were conducted over 2909 km under favourable viewing conditions that included 54 dolphin group follows for 457 km. Sea surface temperature (SST) and chlorophyll-*a* (Chl-*a*) data were obtained from remote sensing imagery, and distances to sources of human influences including fish farms, a ferro-nickel plant, and a slag disposal area were calculated within a geographic information system (GIS).
3. Bottlenose dolphins were encountered mainly in the south-eastern portion of the study area, and occurrence was not clearly related to SST and Chl-*a*, nor the ferro-nickel plant or nearby slag disposal area.
4. Dolphin occurrence generally increased within 20 km of fish farms, with four farms and dolphins displaying a positive relationship, seven no clear relationship, and two a negative one.
5. While it is likely that uneaten food and other detritus attract dolphin prey, individual farms (or clusters of farms) clearly had a different appeal. The proximity of the ferro-nickel plant and slag disposal area to 'attractive' fish farms could compromise dolphin health, but physiological data are unavailable.
6. The modelling of multiple variables allowed for a description of dolphin habitat use and attraction to some fish farms. More such data analysed in similar manner would be instructive for other areas where marine mammals and fish farms co-occur.

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*Correspondence to: S. Bonizzoni. Dolphin Biology & Conservation, via Cupa 40, 06066 Piegaro PG, Italy. E-mail: silvia.bonizzoni@gmail.com

INTRODUCTION

A rising demand for fish products – together with globalization of trade and economic incentives – have resulted in a rapid worldwide increase of aquaculture (Bostock *et al*., 2010). Marine finfish aquaculture, in particular, has greatly expanded in Mediterranean waters (UNEP/MAP/MED POL, 2004; Barazi-Yeroulanos, 2010). Greece is the largest producer of commercial aquaculture finfish species of all European Union and Mediterranean countries (Christofilogiannis, 2010), being responsible for about 40% of the Mediterranean aquaculture production (Katranidis *et al*., 2003). In 2006, approximately 50% of over 30 000 Mediterranean fish farms were in Greece (Trujillo *et al*., 2012). The main species farmed are European seabass *Dicentrarchus labrax* and gilthead seabream *Sparus aurata*, with an estimated yield of 145 000 tonnes in 2008, accounting for over 70% of total aquaculture production (Barazi-Yeroulanos, 2010).

The habitat of common bottlenose dolphins *Tursiops truncatus* (hereafter 'bottlenose dolphins') and other odontocetes overlaps with aquaculture in several coastal areas around the world (Würsig and Gailey, 2002; Watson-Capps and Mann, 2005). In the northern Mediterranean, in particular, bottlenose dolphins have been observed foraging in the proximity of fish farm cages on a regular basis (Díaz López, 2006, 2012; Díaz López and Bernal Shirai 2007; Bearzi *et al*., 2008b; Piroddi *et al*., 2010; Pace *et al*., 2012). Fish farms are known to aggregate wild fish, primarily because of large quantities of uneaten food lost from the cages (Tuya *et al*., 2006; Fernandez-Jover *et al*., 2007). Complex substrate, increased nutrient levels and provision of fish-feed produce trophic enrichment and can attract dolphin prey (Karakassis *et al*., 2000, 2005; Würsig and Gailey, 2002; Kemper *et al*., 2003; Dempster *et al*., 2004). Clarifying the ecological role played by fish farms, as well as the factors that make individual fish farms attractive or unattractive for bottlenose dolphins, can help allocate coastal areas designated for marine aquaculture, so that marine mammal occurrence is taken into account and any potential conflict is minimized.

The Mediterranean subpopulation of the bottlenose dolphin (Bearzi *et al*., 2008b) has been classified as 'Vulnerable' under International Union for Conservation of Nature criteria (IUCN, 2012). Bottlenose dolphins in the coastal waters of Greece have been studied in only a few areas, particularly in the Ionian Sea (Bearzi *et al*., 2005, 2008a). Apart from sighting and stranding reports (Frantzis *et al*., 2003; Frantzis, 2009), there are no published studies on population units inhabiting the Aegean Sea and its adjacent waters. In the Northern Evoikos Gulf, the only information on bottlenose dolphins comes from an unpublished study based on boat surveys and photo-identification of individually recognizable animals (Zafiropoulos and Merlini, 2003). Understanding habitat choice by bottlenose dolphins in Mediterranean coastal waters is essential not only for the conservation management of a protected species, but also to mitigate any negative effect resulting from interactions with human activities.

A generalized additive modelling (GAM) framework was used to investigate factors affecting the distribution of bottlenose dolphins throughout the Northern Evoikos Gulf. In particular, the effects of geographic, bathymetric, oceanographic and anthropogenic variables – including fish farm location and features – that influence habitat preferences by the animals were considered. Taking into account survey effort and sea state conditions, a modelling method inspired by the work of Pirotta *et al*. (2011), which combines visual survey data and dolphin group follows, was used to obtain information on habitat use by the animals. Because dolphin occurrence in the Northern Evoikos Gulf was generally higher near finfish aquaculture facilities, but not all fish farms had the same effects, the possible reasons behind the different potential attractiveness of individual facilities were investigated. The approach presented here can be used to achieve a better understanding of the importance of marine finfish aquaculture for bottlenose dolphins and other species, as well as to investigate fine-scale interactions between dolphins and fisheries.

METHODS

Study area

The eutrophic and productive Northern Evoikos Gulf (Friligos, 1985; Torre *et al*., 2007) is a semi-enclosed basin in central Greece (Figure 1). Trending diagonally north-west–south-east, the Gulf is roughly 80 km long and up to 22 km wide, with a surface area of approximately 960 km^2. Water depths are generally less than 200 m, with a deeper central portion reaching a maximum of 425 m. Such a depression plays an important role as it provides a reservoir where nutrients can be trapped (Friligos, 1985). The Gulf's south-east portion is virtually closed to animal movements due to the narrow Strait of Euripus, which includes two narrower channels 40 and 160 m wide, crossed by bridges. Conversely, the north-west section has a 3.8 km wide mouth, connecting the Gulf to the highly productive Malaikos Gulf and the Oreon Strait, which in turn connects to the Aegean Sea.

The Gulf does not have significant river runoffs and is exposed to considerable human pressures, primarily from heavy industry and fishing. The greatest impact comes from a ferro-nickel smelting plant situated in the town of Larymna (Figure 1). This large plant, active year-round since 1969 and operating 24 hours per day, is the main producer of ferro-nickel in Europe (www.larco.gr). Related environmental issues include pollution from industrial smoke, runoff and disposal of metallurgic waste. The latter concerns the annual production of approximately 2 million tonnes of electric furnace slag (Kirillidi and Frogoudakis, 2005) and the massive daily disposal of slag in adjacent waters of the Gulf, at a rate of 6 tonnes per day (Friligos, 1985; Nicolaidou *et al.*, 1989; Kozanoglou and Catsiki, 1997). High levels of metals have been found in marine invertebrates sampled in this area (Nicolaidou and Nott, 1989; Nicolaidou *et al.*, 1989; Nicolaidou, 1994; Kozanoglou and Catsiki, 1997; Simboura *et al.*, 2000, 2007; Tsangaris *et al.*, 2007; Simboura and Catsiki, 2009), but no information exists about dolphins or other high-order predators. The Gulf's ecosystem is also threatened by intensive fishing, particularly by a large commercial fleet of purse seiners and trawlers (Stergiou, 1999; Katsanevakis *et al.*, 2010a, b). A fleet of trammel and gill netters, as well as longliners, and a few fishing boats using traps also operate in this area. Landings below minimum legal size by purse seiners and trawlers, as well as illegal trawling near the coast, were repeatedly observed during this study, consistent with reports from other areas of Greece (Stergiou *et al.*, 1997, 2007; Bearzi *et al.*, 2006; Piroddi *et al.*, 2010).

Survey effort

Visual surveys were conducted in October 2010 and between March and April 2011 from a 5.8 m

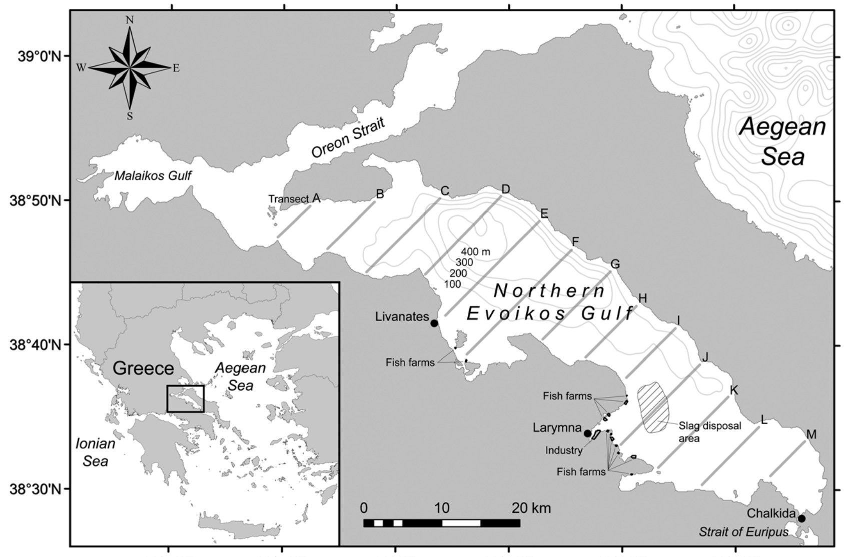

Figure 1. The study area (Northern Evoikos Gulf) situated in central Greece, including 100–400 m isobaths and some of the locations cited in the text. Pre-determined survey transects (A to M) are indicated by parallel lines. Positions of industry, slag disposal area and active fish farms are also shown.

inflatable craft with a rigid hull powered by a 100 HP four-stroke outboard engine, totalling 3340 km of navigation over 39 survey days. Transect lines (A to M in Figure 1) were designed following Dawson *et al*. (2008) to help achieve a more homogeneous and representative coverage of the study area; each transect was covered between 5.3 and 8.7 times (mean = 6.8, SD = 1.02). Dolphin search occurred under the following favourable conditions: daylight (no fog); two experienced observers scanning the sea surface by naked eye; and survey speeds between 28 and 31 km h^{-1}. Navigation under favourable conditions, totalling 2909 km (87% of total effort), is shown in Figure 2. Sea state was categorized as described in the following section. The vessel's position was recorded via GPS at 1 min interval throughout navigation and dolphin group follows (see below).

Effort index and sea state

To account for a different probability of encountering dolphins depending on different effort and sea state conditions, the following two variables were included in the models. A relative sampling effort index was generated by calculating the number of sampling points within stratified grid cells of 3 × 3 km throughout the Gulf, divided by the area of water available within each grid cell (to account for coastal profile). This effort index was then simplified into a factor variable at the quartiles of the resulting values, generating categories of 'low', 'medium', 'high', and 'very high' survey effort. Sea state was also categorized as follows: S1 (flat), S2 (calm but rippled), and S3 (non-breaking wavelets less than 20 cm high, no swell). Data collected with sea states above S3 (i.e. breaking waves) accounted for 16.8% of total favourable navigation and were removed from the analysis due to the low probability of spotting dolphins during these times. Data collected during dolphin group follows under sea states above S3, accounting for 14.9% of total group follows points, were similarly removed from the analysis, to account for inaccuracy under those sampling conditions.

Dolphin group follows

Groups were defined as 'dolphins observed in apparent association, moving in the same direction and often, but not always, engaged in the same activity' (Shane, 1990). Members of the focal group remained within approximately 100 m of each other. When a group separated, one of the resulting groups was followed based on a random choice that was independent of group size or

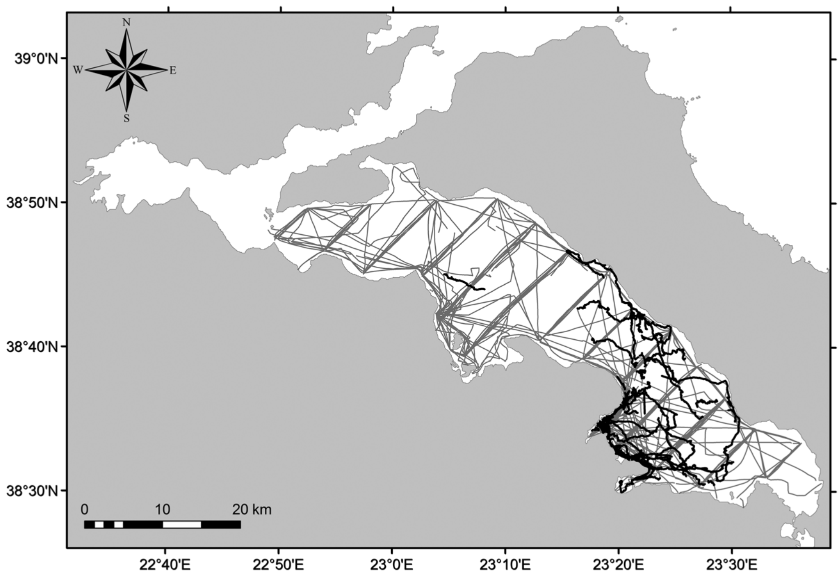

Figure 2. Survey effort under favourable conditions (grey track lines), and movements of bottlenose dolphin groups (black).

activity (Mann, 1999). Dolphin movements were tracked using the vessel's GPS position as a proxy for dolphin position.

Units of analysis

Group follows data were included in the model together with survey data (see Modelling framework section, below). Each 1-min position considered in the modelling was related to a set of variables: latitude and longitude, survey effort, sea state, presence/absence of dolphins, sea surface temperature (SST), chlorophyll a (Chl-*a*), bottom depth, bottom slope, distance to the coast, distance to fish farms, distance to industry, distance to slag disposal area. Following Pirotta *et al*. (2011), all GPS points were divided into individual blocks defined as the set of continuous search points up to a dolphin sighting, or the set of points associated with a dolphin group follow. A new block was also started with each day of sampling. These blocks were then analysed to account for the autocorrelation between residuals within blocks.

Remotely sensed data

Satellite data for SST and Chl-*a* were obtained from NASA OceanColor Web Level 3 Browser (oceancolor.gsfc.nasa.gov) as monthly averages (October 2010, March 2011, and April 2011) MODIS-SMI (Moderate Resolution Imaging Spectroradiometer-Standard Mapped Image) products at 4 km spatial resolution. Bottom depth was obtained from the General Bathymetric Chart of the Oceans (GEBCO08, www.gebco.net) as gridded data at 800 m spatial resolution. All datasets were converted to ArcGIS grid format and then interpolated using ArcGIS topogrid tool at a common spatial resolution of 400 m, a scale consistent with the resolution of the sampled data. Bottom slope (expressed as degrees) as well as distance to the closest coast (m) were calculated via spatial analyst tools using GIS software (ESRI ArcMap 10).

Anthropogenic factors

The Gulf was surveyed visually by boat to assess the presence of finfish cage aquaculture facilities, also considering evidence of fish farm presence as provided by Google Earth (Trujillo *et al*., 2012). In total, 18 fish farms were located; of these, 13 'active' farms had cage nets in place and fish feeding, whereas five had abandoned cage frames with no nets. Farming of European seabass and gilthead seabream was recorded near Livanates (two active farms), in the Bay of Larymna (10 active farms), and in a narrow bay situated south of Larymna (one active farm). The geometry of active fish farms was mapped through a GPS and used to compute farm sizes.

The external perimeter of the ferro-nickel smelting plant (see Study area), derived from Google Earth, was used to define distance to industry. Distance to the slag disposal area was based on georeferencing of a map provided by Simboura *et al*. (2007), which was obtained through 'geophysical seafloor and sub-seafloor imaging systems such as side scan sonar and 3.5 kHz sub-bottom profiler combined with gravity and box coring samples from the area' (p. 167).

All distances to anthropogenic features – fish farms, slag disposal area, and industry – were minimum distances to the perimeter of the feature, taking into account coastal profiles, calculated via spatial analyst tools using GIS software (ESRI ArcMap 10).

Modelling framework

A generalized additive modelling (GAM) framework was used to relate the occurrence of bottlenose dolphins to environmental variables and anthropogenic factors within the Northern Evoikos Gulf. GAMs allow for flexible relationships between the response variable (i.e. dolphin occurrence) and explanatory variables (Hastie and Tibshirani, 1990; Wood, 2006). In the current study, binomial GAMs with a logit link were employed. The logit link function converts the probability of dolphin presence to the natural logarithm of the odds and thus enables this probability to be modelled as a function of the covariates on a linear scale (Matthiopoulos, 2011). In combination with GAMs, generalized estimation equations (GEEs) were used in an approach similar to Pirotta *et al*. (2011) to allow for the use of all collected data. GEEs relax the assumption of independence between model residuals within blocks of data, while maintaining independence among blocks. The relaxed assumption for the residuals within blocks allows for all visual survey and group follow data to be used, without restrictive and subjective subsetting of data. Although specific correlation structures within blocks can be specified, GEEs are robust to model misspecification, and therefore a simple working independence model structure was used, as advised by Pan (2001).

As initial model exploration indicated susceptibility to overfitting, six submodels – each with a set of related variables – were generated to help determine types of factors influencing dolphin occurrence. Generating and evaluating several models rather than a single model allows for 1) comparison among models of relatively equal fit, 2) models to be complementary rather than competing (Planque et al., 2011), and 3) preventing erroneous conclusions about particular effects and their influence on animal distribution (Loots *et al.*, 2011). The organizational framework for submodels is summarized in Figure 3. The geographic submodel initially included latitude and longitude. The bathymetric submodel initially included depth, slope, and distance to coast variables. The environmental submodel initially included two variables: the interaction between SST and season, and chlorophyll *a* levels. Because the water temperatures in the Northern Evoikos Gulf vary widely among seasons, and therefore the relationship between temperature and bottlenose dolphin occurrence may also differ among seasons, the interaction between SST and season was included in the environmental submodel. The anthropogenic model initially included distance to fish farms, distance to slag disposal area, and distance to industry. Each model was examined for multicollinearity before model selection using the variance inflation factor (VIF). All models also included the effort index and sea state variables to account for sampling bias and error.

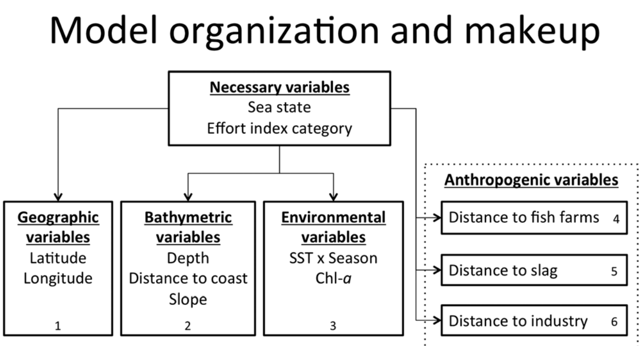

Figure 3. Organizational framework of the six (geographic, bathymetric, environmental, and three anthropogenic) sub-models constructed. All six models contained sea state and effort index category.

GEE-Generalized Linear Models (GEE-GLMs) were constructed with R package (R Development Core Team, 2012), geepack (Yan *et al.*, 2010) and the package splines (R Development Core Team, 2012) were then used to build smoothing splines within the GEE-GLMs, generating GEE-GAMs. The importance of variables within models was investigated by using a manual backward stepwise selection procedure based on minimizing the quasi-likelihood under the independence model criterion (QIC) value (Pan, 2001). QIC values were calculated within the yags package (Carey, 2004) within R 2.14 (R Core Development Team, 2012). Effort index category and sea state factor variables were not subject to stepwise selection and were included in all submodels. To prevent overfitting, each explanatory variable was given a maximum number of degrees of freedom (df) to restrict flexibility as suggested by Ciannelli *et al.* (2008). All models with two or more continuous variables (geographic, bathymetric, and environmental submodels) were constrained to 3 df per continuous fit, while anthropogenic variables were given 4 df to provide more flexibility.

Separate analyses were conducted to determine if and how individual fish farms in the Gulf influenced the occurrence of bottlenose dolphins. In an attempt to observe only local effects and prevent interpretation of impacts acting at larger geographic scales, a subset of the data within 25 km of each individual fish farm was used for each model. This distance approximates the distance at which fish farms seem to influence dolphin occurrence (see Results) while also providing enough data for model stability. As in prior models, index of effort and sea state were included in addition to the distance to a specific fish farm, and each fish farm spline was constrained to 4 df. The resulting 13 response curves, generated in ggplot2 package (Wickham, 2009) indicated whether dolphin occurrence was increased or decreased at each fish farm. Significance ($\alpha = 0.05$) of each fish farm was determined with repeated Wald's tests within the geepack package.

RESULTS

Dolphin occurrence and movements

Bottlenose dolphins were the only cetacean species encountered during the surveys. The movements of 54 dolphin groups tracked during boat follows are shown in Figure 2. Dolphin group follows averaged 94 min (SD = 74.3, $n = 54$, range 2–282), totalling 84 h 20 min and 457 km. Dolphin encounter rates during navigation along transects (ER_t) under favourable conditions and sea states up to S3 ranged between 1.55 and 3.97 groups 100 km^{-1} on transects I, J, K and L, whereas no sightings occurred along the other transects ($ER_t = 0$). Mean encounter rates across the Gulf, based on ER_t values of all 13 transects, was 0.98 groups 100 km^{-1} (SD = 1.564, $n = 13$).

Model output: geographic, bathymetric and environmental variables

For all models, sea state and effort had the same general effect, with calmer sea states (S1) and areas of high effort (categories 'high' and 'very high') increasing the probability of bottlenose dolphin encounters; a representative response plot is given in Figure 4. Within the geographic submodel, longitude was retained while latitude was removed via the QIC model selection procedure. Dolphin occurrence was lower in western portions of the Gulf (west of 23.2°E), however, the confidence intervals around this part of the curve are wide, suggesting that the exact form of the estimated relationship should be interpreted with caution (Figure 5(a)). Within the bathymetric submodel, both depth and distance to coast were retained. The response curve for depth indicates that dolphin occurrence was higher in waters shallower than 300 m (Figure 5(b)), while the response curve for distance to coast shows wide confidence intervals throughout its values (Figure 5(c)). Within the environmental submodel, neither variable (the interaction between SST and season, and Chl-*a*) was retained.

Model output: anthropogenic factors

Because of the high degree of multicollinearity among anthropogenic variables, separate models were generated for distance to fish farms, distance to slag disposal area, and distance to industry to help elucidate the role of anthropogenic effects on dolphin occurrence. A separate model was fitted to each of these anthropogenic impacts, to assess potential differences in the relationships between these factors and the occurrence of dolphins. All models that were generated for analysis resulted in VIF < 5, suggesting that multicollinearity was not an issue within each separate model.

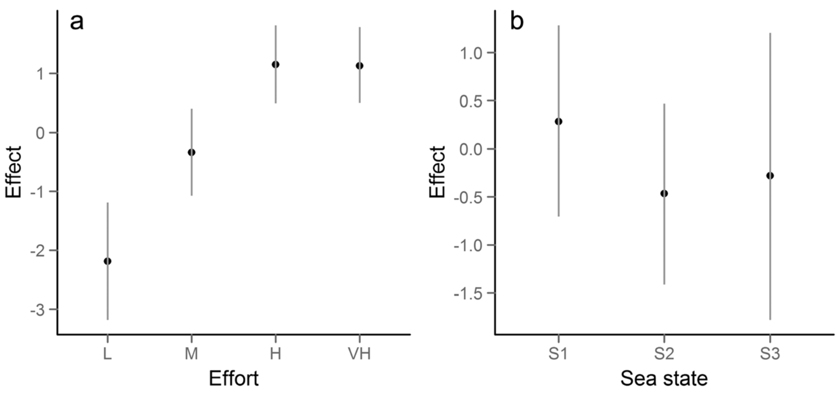

Figure 4. Response plots indicating (a) the relative effect of sampling bias (effort), and (b) sea state on bottlenose dolphin occurrence. Both factors were included in all GAM-GEE models. Grey segments represent 95% CIs as calculated by GEE. L = low, M = medium, H = high, VH = very high. S1 = flat, S2 = calm but rippled, S3 = non-breaking wavelets less than 20 cm high, no swell.

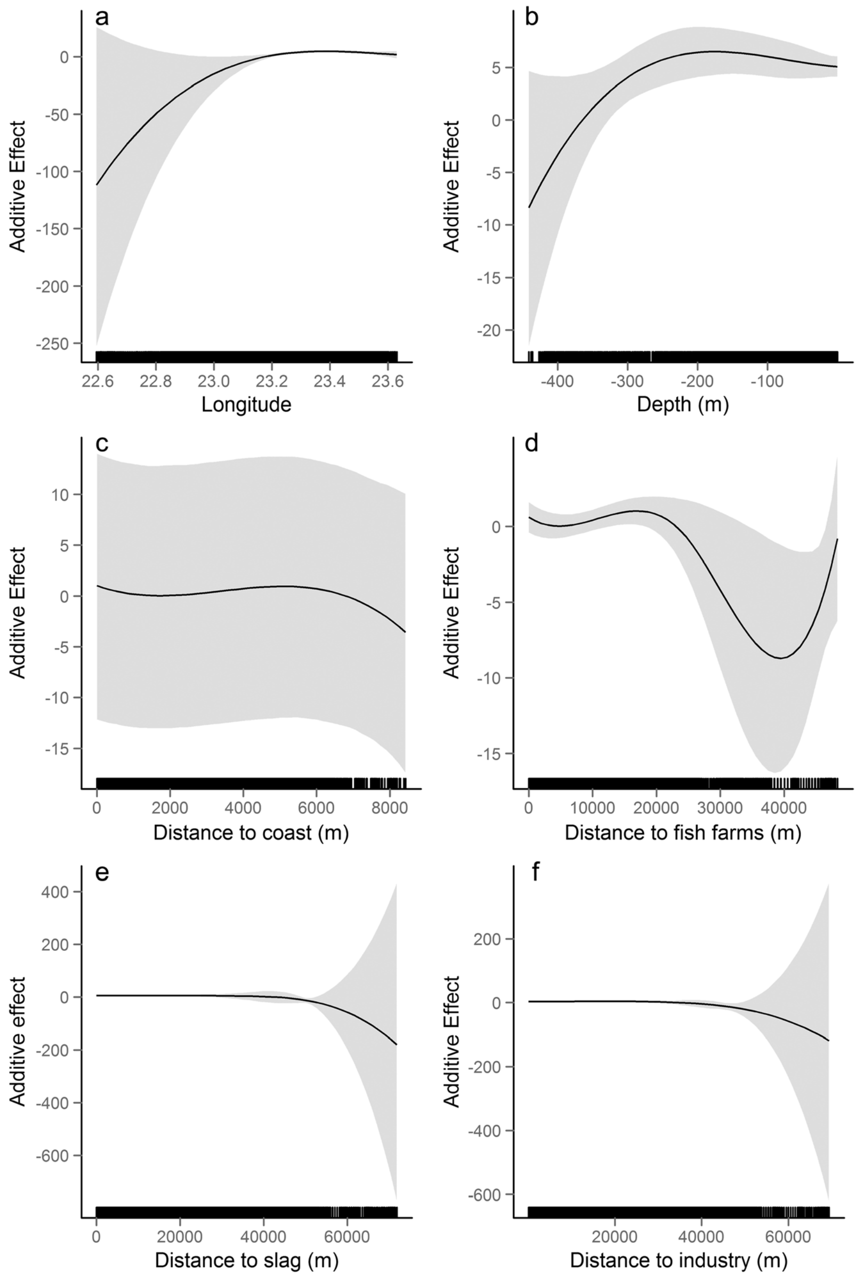

Figure 5. Bottlenose dolphin occurrence modelled as a function of (a) longitude, (b) depth, (c) distance to coast, (d) distance to fish farms, (e) distance to slag disposal area, (f) distance to industry. All distances and depth are expressed in metres. Shaded areas represent 95% CIs as calculated by GEE.

The anthropogenic submodel containing distance to fish farms indicated that bottlenose dolphin occurrence was higher in areas within 5 km of fish farms (Figure 5 (d)), and lower at distances greater than 20 km. Both anthropogenic submodels of distance to the slag disposal area and distance to industry indicated via QIC that these factors were important, with the response curves suggesting that dolphin occurrence was lower at distances approximately greater than 50 km from these features. However, the ranges of distance for which these relationships are negative have wide confidence intervals (Figure 5(e), 5(f)).

Effects of individual fish farms

To examine the relative impact of individual fish farms on a finer spatial scale, data collected within

25 km of each fish farm were run through additional models to look at their influence, and repeated Wald's tests indicated that the distance to six specific fish farms significantly affected bottlenose dolphin distribution in the proximity of farms (Figure 6). Farms F1 and F2 seemed to have a negative relationship, with dolphin occurrence being low within 5 km of either farm; however, the confidence intervals are wide at these distances. Of the other 11 fish farms, four (F3, F4, F5, and F6) displayed significant positive relationships with dolphin occurrence. For farms F3-F6, occurrence declined at distances between 15 and 20 km. F5 and F6, however, demonstrated increased occurrence within 5 km of each site. The remaining seven fish farms (F7 to F13) had insignificant P-values and displayed non-significant relationships with dolphin occurrence within 25 km of their boundaries (Figure 7).

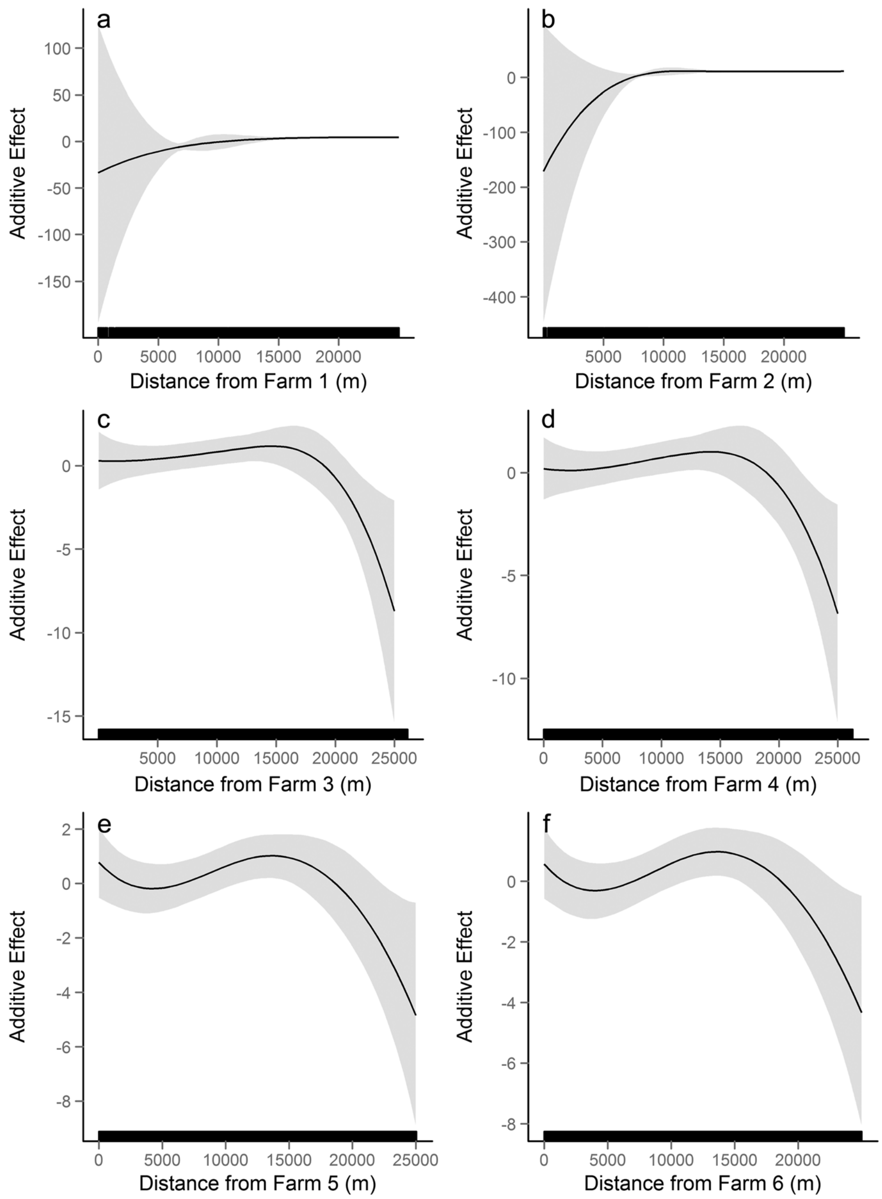

Figure 6. Model output for six fish farms with significant relationships (Wald's test $P < 0.05$) with bottlenose dolphin occurrence. Shaded areas represent 95% CIs as calculated by GEE.

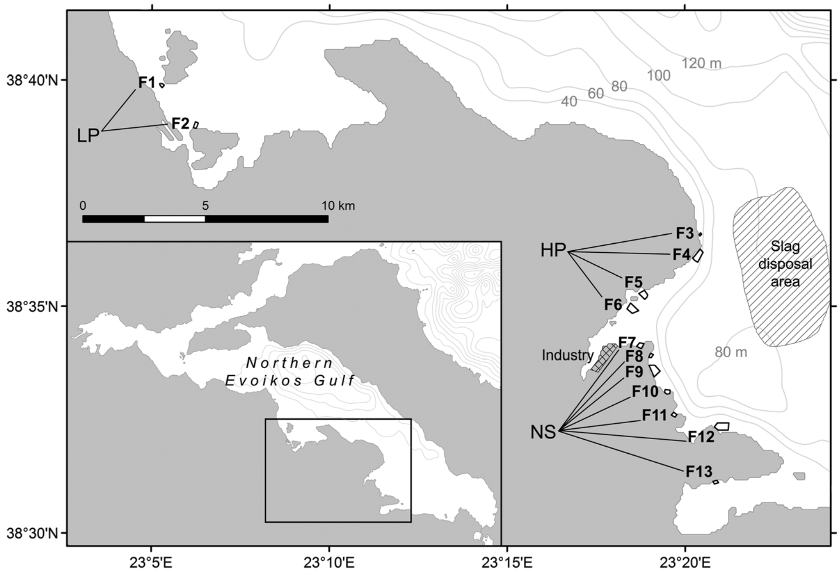

Figure 7. Fish farm locations, along with if they appear to influence bottlenose dolphins based on the GEE-GAMs. The two farms far removed (to the north-west) were associated with lower probability (LP) of dolphin occurrence. Four farms on the coast north of the industry were associated with higher probability (HP) of occurrence. The farms to the east and south of the industry were found to have non-significant (NS) influence on dolphin occurrence.

DISCUSSION

In the Northern Evoikos Gulf, encounter rates as well as tracked movements of bottlenose dolphins suggest a marked preference for the south-east portion (except for the shallow bay north of Chalkida, less than 40 m deep, where dolphins were not encountered). While encounter rates were generally low, dolphins were present at relatively high densities in the section between transects H and L. The modelling framework shed light on the factors likely to affect these habitat preferences.

Sea state and relative effort affect the probability of detecting dolphins (Barlow *et al.*, 2001), and therefore including these variables in each of the models helped prevent spurious outcomes. As expected, the probability of observing dolphins was higher in areas of high survey effort, and when the sea was calm. Geographic and bathymetric variables suggested sub-regional differences in dolphin distribution, with dolphins occurring with a higher probability in the eastern portion of the basin. In addition, bottlenose dolphins seem to avoid the deepest (>300 m) portions of the Gulf, with moderate depths (~200 m) being more likely used than shallower waters. Overall, modelled effects of depth and particularly distance from coast were weak – as could be expected for a relatively small, narrow and semi-closed basin such as the Northern Evoikos Gulf. With regard to environmental variables, at the spatial and temporal scales examined, neither SST nor Chl-*a* concentrations were found to affect dolphin distribution. SST and Chl-*a* are expected to vary on fine spatial scales in areas along the coast and near industry discharge sites, which could impact dolphin distribution by affecting the distribution of their prey items. However, the spatial scale of the environmental data used (4 km) may be too coarse to capture this potentially important variation, especially in coastal areas, where reliability of satellite data is low due to sea–land interaction resulting in mixed or ‘contaminated’ signals received by the satellite sensors.

Of the investigated anthropogenic factors, fish farms appeared to have the strongest effect, with increased bottlenose dolphin occurrence at fish farm locations and in waters within 20 km of fish farms. This confirms previous observations suggesting that areas of fish production are frequently utilized by bottlenose dolphins, and contributes to extend the scant information available as to the impacts of aquaculture on marine megafauna, and vice versa (Würsig and Gailey, 2002; Kemper *et al.*, 2003;

Markowitz *et al.*, 2004; Watson-Capps and Mann, 2005; Díaz López and Bernal Shirai, 2007; Ribeiro *et al.*, 2007). Recent research on the ecological effects of marine finfish aquaculture is mainly related to the dispersal of food given to the farmed fish and to the deposition of waste – such as uneaten food, faeces and dead organisms – in the proximity of the cages (Dempster and Sanchez-Jerez, 2008). Fish farms are known to cause organic enrichment in the sediment (Karakassis *et al.*, 1998) and they can promote changes in the composition and function of benthic communities (Karakassis *et al.*, 2000; Ruiz *et al.*, 2001). They can also attract a great variety of wild fish by providing structure, refuge from predators, and food resources (Dempster *et al.*, 2002; Fernandez-Jover *et al.*, 2007), with influences on wild fish populations extending beyond the immediate vicinity of the farmed area (Machias *et al.*, 2005; Weir and Grant, 2005).

Behavioural observations of individual dolphins conducted during this study were consistent with the hypothesis of fish farms playing a key role in their distribution, as dolphin groups were repeatedly observed performing long dives in the immediate proximity of aquaculture facilities, often within 10 m or less of the cages (Figure 8). In the Bay of Larymna, individuals were also observed surfacing between farm cages with unidentified fish in their mouth. Dolphins spent a considerable proportion of time around fish farm cages, possibly foraging, and then temporarily moved towards deeper waters before returning to the fish farms. No avoidance behaviour by the dolphins was apparent relative to either fish farm infrastructure (cages, cables, pipelines, buoys, etc.) or noise produced by farm workers, boats and aquaculture machinery. These results are in agreement with other studies suggesting that bottlenose dolphins in the Mediterranean have become increasingly accustomed to foraging in the proximity of coastal fish farms (Díaz López, 2006, 2012; Díaz López and Bernal Shirai, 2007; Bearzi *et al.*, 2008b; Piroddi *et al.*, 2010; Pace *et al.*, 2012). This behaviour is probably a response of an opportunistic dolphin species (Shane *et al.*, 1986; Leatherwood and Reeves, 1990; Reynolds *et al.*, 2000) to novel foraging opportunities provided by a growing aquaculture industry, that makes it easier for the animals to exploit a concentrated food source, similar to cases involving trawling (Fertl and Leatherwood, 1997; Chilvers *et al.*, 2003; Ansmann *et al.*, 2012). This behaviour may have evolved culturally (Whitehead *et al.*, 2004) as an adaptation to trophic and other changes such as those having occurred in the Mediterranean marine environment over the past decades (Coll *et al.*, 2010, 2012; Sala *et al.*, 2012). If resources are routinely available, spatially predictable, and appropriately abundant, dolphins can be expected to show some degree of site

Figure 8. Four bottlenose dolphins patrolling fish farm F6, situated close to the ferro-nickel smelting plant in the Bay of Larymna, Greece (photo by G. Bearzi).

fidelity and lower displacement rates (Gowans *et al*., 2007). Local bottlenose dolphins appear to have learned to take advantage of predictable and concentrated prey around fish farms.

The results of this study are unique in that they imply differential use of fish farms by dolphins, with certain farms, or clusters of farms, having remarkably different appeal. GAM-GEE analyses of each individual fish farm indicated that four facilities located north of the ferro-nickel smelting plant (farms F3 to F6 in Figure 7) had a strong positive association with dolphin presence, whereas facilities located to the south did not show significant effects. Furthermore, two fish farms situated in another bay had either a negative effect, or no effect. Different fish farms were compared qualitatively by their size (area), cumulative distance to all other fish farms (as a proxy for fish farm density), distance to ferro-nickel smelting plant, and slope of the underlying bathymetry (Table 1). Fish farm density and slope appeared to play a role in how they affected bottlenose dolphin distribution. Specifically, dense fish farm aggregations (i.e. farms with lower cumulative distance to others) and farms with a gentler (≤2°) slope were associated with a higher probability of dolphin occurrence.

Studies conducted in other Mediterranean areas indicate that similar wild fish assemblages characterize those fish farms located within hundreds of metres to a few kilometres of each other (Dempster *et al*., 2002). Furthermore, fish farms with a high number of cages tend to have higher wild fish abundance, biomass and species diversity (Dempster *et al*., 2002). Clustered farms are therefore likely to aggregate more dolphin prey, making it more energetically efficient for the animals to spend time in that area. In addition, Jusup *et al*. (2007) found that small variations in bathymetry can result in significant changes in sedimentation pattern. An increase in slope can therefore reduce the area affected by nutrients and organic waste, possibly resulting in lower potential for attracting wild fish. Conversely, farms located in areas of even slope may have a lower dispersal of nutrients. The four farms that had increased bottlenose dolphin occurrence were located over less steep bottoms (mean slope of sea bed within 1 km ≤ 2°), than those to the immediate south. There are numerous other factors that may impact affect how individual fish farms are used by bottlenose dolphins. For example, fish farms situated in areas with strong currents have higher dispersion than those in areas of weaker currents (Sarà *et al*., 2004). While current dynamics around individual fish farms could not be investigated in this study, patterns of dispersion and resuspension may play important roles that deserve further investigation. Finally, although fish farms in this study were compared based on some of their main features (i.e. surface area, bottom slope), other characteristics were not considered (e.g. number of cages, fish age within cages, automatic versus manual feeding, etc.)

Table 1. Characterization of the individual fish farms investigated with GAM-GEE models. 'GAM-GEE result' indicates whether individual fish farms had lower probability (LP) of bottlenose dolphin occurrence, higher probability (HP), or non-significant (NS) influence on bottlenose dolphin occurrence. 'Distance to industry' indicates the distance between each fish farm and the industry. 'Fish farm area' indicates the areal coverage of the fish farm. 'Total distance to all other farms' indicates the cumulative distance between the individual fish farm and all other fish farms, and acts as a proxy for fish farm density or relative proximity to all other fish farms. 'Mean bottom slope' was calculated as the mean slope of the bathymetry of waters within a 1 km radius of the fish farm, as interpolated from bathymetry data within a geographic information system (GIS)

Farm	GAM-GEE result	Distance to industry (km)	Fish farm area (m^2)	Total distance to all other farms (km)	Mean bottom slope (%)
F1	LP	31	17,680	340.7	0.4
F2	LP	30.2	30,866	329.5	0.88
F3	HP	5.8	6,308	108.8	2.01
F4	HP	4.9	103,181	102.1	1.98
F5	HP	2.3	69,808	96.4	1.81
F6	HP	1.6	98,730	97.1	1.51
F7	NS	1	40,613	97.2	3.1
F8	NS	2.1	18,853	94.2	2.7
F9	NS	2.7	111,775	95.6	2.4
F10	NS	3.6	32,761	99.6	2.51
F11	NS	4.7	23,706	107.6	2.08
F12	NS	6	149,419	115.4	2.79
F13	NS	11.8	20,372	175.6	1.08

Inclusion of these variables in future studies may increase understanding of the factors that make a farm complex more or less attractive to dolphins.

Acoustic deterrent devices (ADDs) to scare dolphins or other species away from fishing gear (Jefferson and Curry, 1996) are not known to be used by fish farmers in the Northern Evoikos Gulf, and casual interviews with fish farm employees and fishermen yielded no evidence that bottlenose dolphins may depredate or damage farmed fish.

Interpretation of anthropogenic factors other than fish farms, i.e. distance from industry and distance from slag disposal area, is complicated by their partial spatial overlap or proximity with 'attractive' fish farms, as all of these features are found in the same geographic area of the bay (Figure 7). The relationships for bottlenose dolphin occurrence with distance to industry and distance to slag disposal area are very weak, with the negative part of the curves being surrounded by wide confidence intervals (Figure 5). The more descriptive response for distance to fish farms suggests that industry and slag disposal area may only act as proxies of the nearby farms. While increased water temperatures resulting from continuous use of seawater for cooling ashes at the smelting plant may play a role, as could water contamination, noise (e.g. from ship traffic), and the various changes in the ecological community caused by the industry (Nicolaidou *et al.*, 1989; Kozanoglou and Catsiki, 1997), the models do not show apparent effects of being close to either slag or industry sites, and confidence limits at long distances are very wide for both slag and industry, suggesting a lack of confidence in the impact of these factors on dolphin distribution. Furthermore, fish farms situated south of the industry did not seem to affect dolphin occurrence, as they would be expected to do if proximity to industry and slag disposal area played a strong role. Regardless, the models indicate that bottlenose dolphins are in close proximity to both the industry and slag disposal area, irrespective of cause.

While bottlenose dolphins may not avoid or be attracted to industry or the slag disposal area, it is likely that exposure to polluted waters, polluted prey and/or noise can result in long-term negative impacts on the animals. Several individuals photographed during this study showed tumours, body deformities and skin diseases, to an extent not found in other parts of the Mediterranean Sea where some of the authors have been studying bottlenose dolphins (for up to 25 years). The consequences of feeding around fish farms situated in coastal waters exposed to heavy industry noise, smoke, runoff and large-scale disposal of metallurgic waste is a conservation concern, and more information is needed to assess long-term impact on the population dynamics of bottlenose dolphins. In addition, the close proximity of fish farms, industry, and the slag disposal area may pose threats that extend beyond ecology of the region, in the form of the quality of fish produced at fish farms that are in turn consumed by humans (Sapkota *et al.*, 2008).

This study suggests that fish farms have a differential impact on bottlenose dolphin behaviour and distribution, but more work is needed to explain confidently what makes some farms uniquely appealing to bottlenose dolphins. Detailed data about water circulation, SST *in situ*, substrate type, waste distribution, fish farm activity and productivity, distance from the pens to the sea bed, number of cages, etc., would help elucidate the forces that can affect dolphin occurrence. In addition, these studies should be replicated year-round in other areas and in more open (or more enclosed) waters to elucidate local and seasonal variability. For instance, limited water exchange in semi-enclosed gulfs may result in a more apparent environmental impact than is found in farms under semi-exposed conditions (Neofitou *et al.*, 2010). Furthermore, investigations are needed to understand better the impacts of fish farm utilization on bottlenose dolphin ecology, especially in situations where fish farms are in close proximity to sources of intense pollution.

While no direct conflict was apparent in the Northern Evikos Gulf, such conflict may develop rapidly if the animals learn to take advantage of the caged fish. For instance, a study in the central Mediterranean reported a few cases of bottlenose dolphins 'biting the nets of the cages, causing direct damage to farmed fish as they attempted to remove them' and 'damaging the nets in the form of small holes' (Díaz López, 2006, p. 308). The subsequent deployment of anti-predator nets caused dolphin mortality (Díaz López and Bernal Shirai, 2007; Díaz López, 2012). In addition, dolphins may be blamed for causing stress to the farmed fish, although there is no evidence to support such claims (Díaz López, 2006; Bearzi *et al*., 2008b). Because actual, inferred or perceived damage caused by dolphins or other animals may result in retaliation or deployment of inappropriate devices by the farmers (e.g. shooting, anti-predator nets, acoustic deterrent devices), appropriate monitoring and – in case of need – the prompt enforcement of site-specific management actions are needed to ensure that dolphins and fish farms can operate together without undue conflict.

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