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Investigating food-web interactions between Mediterranean coastal dolphins and fisheries in "natural laboratories"

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INTRODUCTION

This paper aims (1) to summarize current knowledge about the potential impact of prey depletion and nutritional stress¹ in Mediterranean cetaceans, (2) to make recommendations about how to investigate this problem into further detail, and (3) to propose the semi-enclosed waters of the Amvrakikos Gulf, north-western Greece, as a promising "natural laboratory" where ecological interactions between common bottlenose dolphins (*Tursiops truncatus*) and fisheries can be investigated.

CETACEAN PREY DEPLETION IN THE MEDITERRANEAN SEA

Jackson *et al.* (2001) argued that "ecological extinction caused by overfishing precedes all other pervasive human disturbance to coastal ecosystems, including pollution, degradation of water quality, and anthropogenic climate change". This lesson may also apply to the Mediterranean, where fisheries have had major direct and indirect impacts on ecosystem dynamics (e.g. CIESM, 2000; FAO, 2000).

The poor state of several Mediterranean fish stocks and the inadequacy of the current exploitation pattern to secure sustainable fisheries have been repeatedly pointed out by the scientific community. Although Mediterranean fisheries statistics are incomplete and unreliable, and there is an acute lack of historical data (CIESM, 2000, 2003), unsustainable harvesting has led to the decline of many fish stocks (Caddy and Griffiths, 1990; De Walle *et al.*, 1993; Stanners and Bourdeau, 1995; CIESM, 2000; FAO, 2000), with potentially serious ecological consequences (cf. Dayton *et al.*, 1995; Jackson *et al.*, 2001). A recent document by the EC concludes that overall production and catch rates in the Mediterranean have been steadily decreasing, despite the increase in fishing effort, as compared with yields obtained 20 or more years ago. For example, in some of the most productive areas such as the Adriatic Sea and the strait of Sicily, overall catch rates per unit of effort were said to have diminished by more than 60% (EC, 2003).

¹ Trites & Donnelly (2003) defined nutritional stress as a negative physiological and/or behavioural state resulting from suboptimal quantity or quality of food available to an animal. Effects of and responses to nutritional stress in terrestrial and marine mammals include reduced body size, reduced birth rates, increased neonate mortality, increased juvenile mortality, behavioural modifications (e.g. longer foraging bouts), and changes in blood chemistry and body composition.

The mean trophic level of Mediterranean catches was reported to have declined significantly and quite steadily since the late 1950s, although aggregate fishery landings have increased (e.g. Pauly and Palomares, 2000; Stergiou and Koulouris, 2000). Although there is an ongoing debate on whether such a trend is occurring in the whole Mediterranean (e.g. see Pinnegar *et al.*, 2003), a pervasive and large-scale "fishing down" impact on marine food webs (Pauly *et al.*, 1998a) would have a profound impact on ecosystem dynamics, ultimately affecting top predators.

Overfishing, as well as habitat degradation, has been proposed as a factor that may significantly contribute to the decline of Mediterranean cetaceans - particularly coastal dolphins - by reducing the availability and/or the quality of their prey (Bearzi, 2002). As stressed by Chapman and Reiss (1999), the lack of sufficient food to maximise reproductive potential may be the most important regulator of population size in animals. Unfortunately, it is highly difficult to determine to what extent nutritional stress is a contributing factor to the decline of any particular population. The "nutritional quality" of a diet is a complex matter and the effects of different diets on animal health are particularly difficult to assess in free-ranging cetaceans. Just how large the nutritional deficit must be to noticeably affect blood chemistry, behaviour, growth, survival and reproduction is not known; nor is it known if these changes occur in progressive and predictable manners (Trites and Donnelly, 2003).

However difficult it may be to establish a clear, mechanistic link between fisheries exploitation and the decline of some cetacean species, such a link provides one of the most plausible contending hypotheses for coastal odontocetes (Bearzi, 2002). Exploitative competition with fisheries represents a source of concern in all the Mediterranean areas where short-beaked common dolphins *Delphinus delphis* have been studied consistently, including the eastern Ionian Sea, the south-eastern Tyrrhenian Sea, and the Alboran Sea (Bearzi *et al.*, 2003). Prey depletion resulting from overfishing and habitat degradation is also one of the likely causes that prompted the disappearance of common dolphins from the northern Adriatic Sea, where these animals used to be regular until the 1970s (Bearzi *et al.*, in press).

When mass mortality events occur, prey depletion and xenobiotic contamination are often mentioned as potentially contributing factors having compounding effects. For example, inadequate nutrition may have compromised animal health and made Mediterranean striped dolphins *Stenella coeruleoalba* more susceptible to the epizootic that caused a large die-off in 1990-1992 (Aguilar and Raga, 1993; Aguilar, 2000).

In the Black Sea, reduced prey availability has been cited as a factor affecting the abundance of common dolphins and harbour porpoises Phocoena phocoena (Bushuyev, 2000). Of two mass mortality events involving Black Sea common dolphins in 1990 and 1994 (Krivokhizhin and Birkun, 1999), only one was recognised as being the result of a morbillivirus epizootic (Birkun et al., 1999). Most stranded animals (dead and alive) examined during both die-offs were emaciated (A. Birkun, pers. comm.). Although such emaciation could be a result of the disease, both die-offs coincided with steep declines of European anchovy Engraulis encrasicolus and European sprat Sprattus sprattus stocks, the main prey of Black Sea common dolphins (Birkun, 2002). Overfishing, combined with the consequences of eutrophication (e.g. water hypoxia) and the concurrent irruption of the introduced ctenophore *Mnemiopsis leidvi*, has been blamed for the rapid decline in anchovy and sprat stocks (Zaitsev and Mamaev, 1997). The total commercial catch of anchovies experienced a 12-fold decline (from an absolute maximum of 468,800 tonnes in the 1987-1988 fishing season to 39,100 tonnes in 1990-1991), while landings of sprat fell by a factor of nearly eight (from 105,200 tonnes in 1989 to 13,800 tonnes in 1993; Prodanov et al., 1997). This suggests a close relationship between large die-offs of Black Sea common dolphins and prey scarcity (A. Birkun, pers. comm.).

Mediterranean fisheries are now exploiting most of the fish and fishing grounds available down to a depth of more than 800 metres. The gradual extension of fishing activities to off-shore fishing grounds, exploiting either new stocks or new parts of already over-harvested stocks, have the potential for threatening the food resources of pelagic cetacean species which so far may have been relatively unaffected by prey depletion. Exploitation of deeper fishing grounds would be particularly dangerous, due to the low productivity of such biological systems (which makes deepwater fish more vulnerable to fishing) and to the presence of important but not yet well identified habitats (EC, 2003).

INVESTIGATING NUTRITIONAL STRESS IN CETACEANS

Work done on pinnipeds in recent years is especially valuable to indicate how the issue of nutritional stress may be approached. For instance, research conducted in Alaska by Trites and Donnelly (2003) has shown that declining Steller sea lion (*Eumetopias jubatus*) populations were nutritionally compromised because of the quality of prey available to them (chronic nutritional stress), rather than because of the overall quantity of fish *per se* (acute nutritional stress). This suggests that prey *quality* is at least as important as *quantity* when it comes to evaluating the potential impact on the animals - a consideration that so far has been overlooked in most cetacean studies.

Energetic requirements of top level predators can be used to infer the probable ecosystem structure. Energy consumption by cetaceans can be based on the number of individuals present in a given area at any time, their trophic level, the food requirements of each individual, and the rates of energy transfer between trophic levels (Hooker *et al.*, 2002a). Although it is difficult to perform studies on cetaceans similar to those carried out on pinnipeds (e.g. based on blood chemistry, accurate body size measurements etc.), viable research approaches can be identified to evaluate nutritional stress in free-ranging cetaceans through non-invasive techniques. To this regard, a multi-disciplinary approach based on a combination of research methods may provide valuable results.

A variety of different methods can be used to gain insight into what cetaceans eat. These include the following ones, each presenting advantages and disadvantages (e.g. see Barros and Clarke, 2002):

1) Intestine and stomach contents in stranded or bycaught animals can be studied to identify the structures representing a typical meal, e.g. fish bones and the jaws of cephalopods. Fish otoliths and lower cephalopod beaks, in particular, are diagnostic structures in the identification of prey (Barros and Clarke, 2002).

2) Systematic behavioural sampling and the study of surfacing patterns by focal individuals may provide insight on preferred prey type (e.g. epipelagic vs. demersal), and help assessing the time devoted to feeding and the related energy investment as compared with temporal and environmental variables (Fortuna *et al.*, 1998; Bearzi *et al.*, 1999).

3) Isotopes in biopsy samples can be analysed to obtain information on cetacean prey preferences (e.g., Todd *et al.*, 1997), as well as on food preferences by other ecosystem components (Das *et al.*, 2000; Polunin and Pinnegar, 2000; Lesage *et al.*, 2001). Remotely-obtained skin biopsies may be used in isotope analysis and thus provide an alternative to the examination of stomach contents to delineate diet. Dietary evaluations based on analyses of assimilated tissues implies that the data reflect dietary information integrated over a longer period of time, as opposed to the instantaneous sampling of recently digested food items. With the added possibility of re-sampling photo-identified individuals between seasons or years, isotope analysis may also be used in longitudinal studies of foraging behaviour (Todd *et al.*, 1997). Stable isotope analyses performed on teeth from museum collections and stranded individuals may provide comparative insight on the diet of modern *versus* historical cetacean populations (Walker and Macko, 1999; Walker *et al.*, 1999).

3) Fatty acids analysis can be useful in reconstructing changes in diet (e.g. Hooker *et al.*, 2001), although this method presents shortcomings related to fat stratification in the outer and inner blubber layer, which may yield misleading results of dietary information (Barros and Clarke, 2002).

4) Finally, biochemical analyses of lipid contents/structure in blubber from biopsies may, in the future, help detecting starvation or nutritional stress.

Information collected through "traditional" studies can also be directly or indirectly relevant to nutritional and ecosystem studies. For instance, individual photo-identification (Hammond *et al.*,

1990) may help assessing population numbers and dynamics, habitat use, immigration rates, calving and survival rates, and a number of other key biological features including information on the physical appearance of known individuals over time (e.g. emaciated vs. well-fed, Politi *et al.*, 2000). Genetic studies performed on swabbed skin samples (Harlin *et al.*, 1999) or stranded animals may help assessing - among other things - genetic variability and the degree of isolation of a given cetacean community, which can represent relevant background for food-web studies.

In addition to the approaches described above, ecosystem modelling has been proposed in recent years as a viable tool for understanding the complex ecological interactions between cetaceans, fisheries and other ecosystem components (e.g., Smith, 1995; Earle, 1996). For effective conservation policy it is widely recognized that an ecosystem-level approach is more effective than that at species-level (Agardy, 1994; Jones, 1994). However, such an approach is often difficult. Theoretically, an ecosystem should encompass all the linkages between species within a defined habitat, but the spatial boundaries of marine ecosystems are mostly nebulous. Ideal "natural laboratories" for ecosystem studies focusing on coastal cetaceans may be represented by semiclosed systems with low rates of immigration and emigration, where cetacean numbers, age classes and diet, as well as prey quantity and removal rates by fisheries can be determined more precisely than in open systems.

With proper development and implementation, and applied on systems for which sufficient information exists, software tools such as "Ecopath-Ecosim" (Christensen and Pauly, 1992) may increase our understanding of food-web dynamics and future cetacean management. Models can provide information on food consumption of cetaceans as compared with fisheries catches, and indicate the degree of resource overlap (Kaschner *et al.*, 2001). This approach to the study of marine food webs and cetacean-fisheries interactions may help identify areas of conflict and serve as a useful management tool in the context of defining critical habitat for cetaceans.

DEALING WITH COMPLEXITY

As discussed above, the complexity of marine food webs and a troublesome access to the relevant data make it difficult to provide conclusive evidence that nutritional stress represents a threat to cetaceans. Prey depletion may be a subtle and scarcely noticeable threat, and the impacts may go unnoticed owing to inadequate research effort (e.g. monitoring changes in reproductive success or

survival rates). Even in places where the research effort has been extensive, it is difficult to find simple cause-effect relationships between dolphin trends and prey availability.

For instance, bottlenose dolphins and common dolphins were studied intensively around Kalamos, north-western Greece (Figure 1), between 1993-2003. A total of 25,000 km of navigation on effort conducted during 800 boat surveys allowed to document a significant and continuous decline in the density of common dolphins since 1997, and generally low densities of bottlenose dolphins. The most likely causal factor to explain the observed trends appears to be a decline in prey availability over time (Politi and Bearzi, in press; Bearzi, 2003). However, the open character of this marine ecosystem makes it difficult to relate changes in prey abundance and dolphin trends. Food-web studies are complex in this area due to factors including inter alia: 1) the observed dolphin move-



Fig. 1. The semi-enclosed Amvrakikos Gulf and the open waters surrounding the island of Kalamos, north-western Greece. The areas where dolphin studies have been conducted are indicated in light grey.

ments in and out of the main study area, making actual movement ranges by the dolphins unknown; 2) a documented presence of transient bottlenose dolphins using the area on occasional bases; 3) possible "food-web" competition between the two dolphin species; 4) presence of other top predators (tuna, swordfish etc.) overlapping in diet with common dolphins; 5) high and largely unpredictable rates of immigration/emigration for most pelagic species; 6) difficulties to monitor fishery trends (e.g. landings refer to a wider fishing area, and CPUE data are unavailable); and 7) poor or absent background information on other trophic levels, e.g. to implement ecosystem models.

In conclusion, despite the abundant longitudinal data collected on dolphins, it is currently difficult to bring conclusive quantitative evidence that overfishing in the area of Kalamos - a well-documented fact (Papaconstantinou *et al.*, 1985a,b; Papaconstantinou *et al.*, 1988; Papaconstantinou and Stergiou, 1995; Stergiou *et al.*, 1997) - is responsible for the observed decline of common dolphins. So far, such an hypothesis rests upon consistent indirect evidence and common sense. Part of the difficulties relate to the fact that the area of Kalamos does not represent an ideal "natural laboratory" for this kind of studies.

THE AMVRAKIKOS GULF, GREECE: A "NATURAL LABORATORY" FOR THE STUDY OF FOOD-WEB INTERACTIONS BETWEEN BOTTLENOSE DOLPHINS AND FISHERIES

Although the inherent complexity of food-web dynamics often makes it difficult to investigate the role of cetaceans in the ecosystem and to evaluate the ecological significance of competitive interactions with fisheries, insightful studies can be conducted in semi-closed marine systems.

The Amvrakikos Gulf, situated in north-western Greece (Figure 1), is virtually a closed basin whose only channel to the open Ionian Sea is a narrow and shallow canal 600m wide, which renews the waters of the Gulf very slowly through a process that takes nearly one year to complete. The Gulf - roughly 400Km² - stretches over an area of approximately 60Km, and its waters have a maximum depth of 60m. As a result of the high input of nutrients due to river runoff, the Gulf is among the most productive coastal areas of Greece.

Research conducted by the Tethys Research Institute since 2001 in the context of a long-term monitoring programme confirms that an abundant bottlenose dolphin "community" (*sensu* Wells *et al.*, 1987) lives in the Gulf. Based on three years of photo-identification work (>2,500 dorsal fin photos filed and about 60 individuals identified between 2001-2003), these dolphins show high levels of site fidelity². Individual movements in and out of the Gulf appear to be limited, probably owing to dramatic differences between the shallow, highly productive, turbid waters of the Gulf and the deep, oligotrophic, limpid Ionian Sea open waters. The bottlenose dolphin community living in Amvrakikos clearly benefits from abundant prey resources, as shown by behavioural observations within the Gulf. Conversely, in the nearby open waters of the eastern Ionian Sea bottlenose dolphin densities are low (Politi *et al.*, 1992) and prey shortage is an issue (Politi *et al.*, 2000; Bearzi, 2003). The data collected so far indicate that bottlenose dolphin densities in Amvrakikos are one order of magnitude higher than those recorded at Kalamos.

Bottlenose dolphins in Amvrakikos - as well as the locally abundant sea turtles *Caretta caretta* - are blamed for inflicting damages to fishing gear, thus causing significant loss to local fishermen. Dolphin and turtle attacks are claimed to have increased in the last decade, together with depredation by cormorants *Phalacrocorax carbo* (Athanassopoulos *et al.*, 2003), but no compensation mechanism has been put in place by the Greek government. Gear and fish losses embitter the problems experienced by local fishermen, who lament that the local production has declined and the cost of fishing has become excessive in recent years (Conides *et al.*, 2001). Artisanal fishermen claim that commercial overfishing jeopardizes the resources in the Gulf. Illegal fishing by non-local fleets, in particular, is blamed by some for the decline of the shrimp *Penaeus kerathurus*, one of the most profitable fishery targets. Pollution from rivers has also been related to shrimp decline (Conides *et al.*, 2001).

² Consistent results were obtained by Zafiropoulos & Merlini (unpublished abstract, see http://www.efm-sts.org/files/Zafiropoulos.pdf).

Jackson and Sala (2001) argued that, today, our ecological understanding of most marine systems is biased by a misperception of what was their pre-exploitation state. Because of a phenomenon described by Pauly (1995) as the "shifting baselines" syndrome of fisheries, it is difficult to frame ecosystem changes into the right context once its original state has been dramatically changed by overfishing. Although some evidence of habitat degradation has been recorded in the last decade, the Amvrakikos Gulf is a very productive area where the "fishing down" phenomenon, if present, is likely to be in its early years. Compared with the Mediterranean scenario, particularly as far as lagoons and coastal systems are concerned, the Amvrakikos Gulf still sustains abundant resources and a large community of top predators. Therefore, this semi-closed basin may be particularly appropriate for conducting longitudinal studies aimed at investigating food-web interactions and changes in dolphin population dynamics.

Ecosystem studies highlighting the roles of cetaceans would be relatively simple here as 1) there is only one cetacean species; 2) there seem to be no large top predators with diets overlapping those of the dolphins; 3) shark predation on dolphins is probably insignificant; 4) bottlenose dolphins appear to be present year-round, and their movement ranges are probably limited to the Gulf area; 5) rates of immigration/emigration are absent or low for many of the other species living in the Gulf; 6) it is easy to study dolphins due to their high densities; 7) it should be relatively easy to monitor fishery landings and trends within the Gulf area; and 8) reasonably good background information exists on other trophic levels, which facilitates ecosystem modelling.

Therefore, the semi-closed Amvrakikos Gulf appears particularly appropriate for conducting studies aimed at investigating food-web interactions and changes in dolphin population dynamics based on the methods described elsewhere in this volume. This would result in increased understanding of trophodynamics which might benefit cetacean and ecosystem studies in other areas. For instance, data obtained in the Gulf can be compared with information on the well-studied bottlenose dolphins living outside the Gulf, in the oligotrophic waters around Kalamos. Comparisons between these geographically contiguous but likely separated bottlenose dolphin communities may focus on diet differences, nutritional status (including relative occurrence of emaciated individuals; Politi *et al.*, 2000) and proportions of time spent in feeding-related activities.

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