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ORIGINAL PAPER

The functional significance of colouration in cetaceans

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Abstract Cetaceans show many of the classic mammalian colouration patterns, such as uniform colouration, countershading, and prominent patches of colour, all within one relatively small taxon. We collated all the functional hypotheses for cetacean colouration that have been put forward in the literature and systematically tested them using comparative phylogenetic analyses. We found that countershading is a mechanism by which smaller cetacean species may avoid being seen by their prey. We discovered that prominent markings are associated with group living, fast swimming, and ostentatious behaviour at the surface, suggesting that they function in intraspecific communication. White markings on several parts of the body seem to be involved in the capture of fish, squid, and krill. Therefore, several different selection pressures have shaped the great diversity of skin colouration seen in extant cetaceans, although background matching, disruptive colouration and interspecific communication do not appear to be involved.

Keywords Colour · Countershading · Distinctive marks · Whales

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Introduction

Although theories of animal colouration were developed principally in regard to terrestrial species (Wallace 1879; Poulton 1890; Cott 1940; Edmunds 1974), from early on they were applied to aquatic species too (e.g., Wallace 1889; Beddard 1895; Longley 1916, 1917). Nonetheless, colouration of aquatic organisms is subject to different selection pressures than those operating on land because scattering of light in water leads to an unchanging angular distribution of light direction; light only penetrates surface waters, the extent to which additionally depends on turbidity; light may be refracted at the surface; and species that use the water column may be viewed by prey, predators or conspecifics from almost any angle (Lythgoe 1987; Marshall 2000; Hanlon et al. 2009; Zylinski et al. 2009). These properties favour certain mechanisms of crypsis including transparency, counter illumination and countershading (Johnsen 2001; Johnsen et al. 2004; Ruxton et al. 2004). For example, countershading, in which the dorsal surface of the individual is usually dark but the ventrum is light, is thought to operate particularly effectively when light streams in from above and predators approach prey from the side because this form of colouration may serve to counterbalance differences in shade produced by the body itself (self-shadow concealment, Kiltie 1988; Rowland 2009). While we know that countershading, transparency, and other traits such as bioluminescence, are present in many aquatic organisms, only very rarely has the distribution of these traits across species been related to environmental or social factors and this constrains our understanding of the evolutionary drivers of animal colouration in marine and freshwater habitats. In contrast, associations between patterns of colouration and various aspects of ecology have now been explored comparatively in several terrestrial mammalian taxa including carnivores (Ortolani and Caro 1996; Ortolani 1999), lagomorphs (Stoner et al. 2003a), artiodactyls (Stoner et al. 2003b; Caro and Stankowich 2009) and primates (Kamilar 2009). Here we examine these associations in whales, dolphins and porpoises, an entirely aquatic group that show great diversity in their colouration patterns, and in so doing extend knowledge of the functional significance of colouration in mammals.

Cetaceans are divided into the baleen whales (Mysticeti) that filter food from water, and the toothed whales, dolphins and porpoises (Odontoceti) that use echolocation to detect prey, which they capture by suction or tooth-assisted predation (Fordyce and de Muizon 2001). There is a formidable literature on cetacean biology: colouration patterns are well described; behavioural observations include in-depth studies which in conjunction with anecdotal data form a reasonably robust dataset on species' social and environmental variables; and there are good morphological and molecular phylogenies available with which to test hypotheses about colouration (e.g., Messenger and McGuire 1998; Geisler and Sanders 2003; Price et al. 2005; McGowen et al. 2009).

The disadvantages of working with this taxon are that most species utilize a range of depths and light environments because they must all come to the surface to breathe; some species observe each other both above and below the water's surface opening up the possibility that colouration may be under selection in at least two lighting environments; new species of beaked whales have been discovered recently but little information is available on their behavioural ecology; and information on the colour of some species is based on artists' drawings of dead specimens rather than photographs of live animals. Despite these provisos, the cetaceans provide a test case for exploring the evolution of colouration in a marine environment and plug an important gap in understanding the evolution of colouration in mammals more generally. In the next section we collate all the diverse hypotheses and anecdotes that have been put forward to explain specifically the function of colouration in cetaceans.

Hypotheses for colouration in cetaceans

Whale colouration has attracted people's interest and imagination for centuries. For example, the central character in Herman Melville's (1851) novel Moby Dick was an unusually coloured pure white sperm whale *Physeter macrocephalus* aka *catadon*; but scientific discussion of colouration in cetaceans only began seriously with Yablokov (1963). He divided colouration patterns into three types: uniform or finely spotted; countershaded; and strongly spotted, striped or patterned. These, he thought, were respectively (1) adaptations to feeding on plankton, or living in murky or deep water where vision was difficult or unimportant; (2) camouflage against predators when foraging near the surface; and (3) for intraspecific recognition. Since 1963, hypotheses have become somewhat more refined in terms of explaining function and more precise in detailing where distinctive marks are located on the body. In addition, we now know that whales generally lack blue retinal cones and so are green cone monochromats, probably making them colour blind (Griebel and Peichl 2003).

Uniform and spotted colouration

According to Yablokov (1963) and Wursig et al. (1990), uniform dark colouration might be a form of crypsis and should be found in species that live in places where little light penetrates. Another idea is that uniformly spotted colouration might be a form of crypsis specifically against fish and squid prey that use vision to detect and avoid predators (Mitchell 1970; Perrin 2009). Regarding spotting, there is agreement that the extent and intensity of spots increases with age and sexual maturity in *Stenella* and *Tursiops* species (Perrin, 1970; Kasuya et al. 1974; Hohn et al. 1985; Myrick et al. 1986; Ross and Cockcroft 1990; Smolker et al. 1992; Herzing 1997). We set out to test whether uniformly coloured cetaceans live in low light environments based on depth or turbidity and whether spotted cetaceans eat fish or squid prey.

Countershading

Countershading in cetaceans incudes both a smooth gradation between a dark dorsum and a light ventrum, as in the Atlantic hump-backed dolphin *Sousa teuszii*, as well as a sharp division of dark and light occurring near the midline of the flank, as in the Atlantic white-sided dolphin *Lagenorhynchus acutus*. Smooth countershading (that ranges from subtle to obvious) and sharp countershading may be different methods of crypsis: the former a form of self-shadow concealment, the latter a form of background matching. Some of the functional ideas that have been put forward for countershading in cetaceans are that it is used to evade predation (Wursig et al. 1990) or to avoid being seen by fish and squid prey that have good visual acuity (Wursig et al. 1990). Hypotheses for countershading being a form of self-shadow concealment predict that countershading will be found in species that live in conditions of relatively strong directional light near the surface (Hailman 1977) or that feed in the photic zone on nektonic organisms (Yablokov 1963). Put another way, countershaded species will not be found in inshore silt-laden waters or in productive waters with uniform lighting (Munz and McFarland 1977; Wursig et al. 1990). We tested whether countershaded species inhabit well-lit environments, whether they are small and thus subject to higher predation pressure (Kamilar 2009), and whether they feed on fish and squid prey.

Prominent markings

Many cetacean species have distinct patches of white skin on an otherwise dark background, and some authors have suggested that this form of colouration disrupts the outline of the body especially in well-lit environments (Hailman 1977) or, more specifically, in clear waters subject to flickering sunlight (Munz and McFarland 1977; Wursig et al. 1990). Note, these ideas about disruptive colouration do not distinguish between avoiding predation or avoiding attention of prey. We tested whether prominent marks might serve to disrupt the body's outline indirectly by examining whether such species inhabit well-lit environments.

Alternatively, prominent marks on cetaceans may facilitate communication between conspecifics. Arresting marks, especially white marks, or sharp boundaries seen in some forms of countershading, are thought to be involved in social behaviour either because they mediate individual recognition (Yablokov 1963; Mitchell 1970), or they are involved in group cohesion (Heyning 1988; Wursig et al. 1990), or they are used to signal to conspecifics (Wursig et al. 1990). As a consequence, outstanding markings might help to coordinate group movements (Norris and Schilt 1988). A separate hypothesis is that white areas below the jaw line are a means of exaggerating tooth size in the context of sexual competition (Heyning 1984).

Furthermore, prominent markings are also hypothesized for use in interspecific communication, for example, as a means of distinguishing conspecifics from heterospecifics in cetacean species that commonly associate together (Norris and Dohl 1980; Heyning 1988). A second heterospecific communication idea derives from Wursig et al. (1990) who suggest that distinctive marks might confuse predators, or confuse prey. More specifically, Wilson et al. (1987) argue that conspicuous colouration is found in species with a diet of pelagic prey because it serves to break up schools of fish—perhaps through disorientation or confusion of prey—making their capture easier. Finally, hourglass patterns on cetaceans may disguise the outline of a calf swimming next to its mother from potential predators (Yablokov 1963; Mitchell 1970). We tested for an intraspecific communication function by matching prominent marks to several measures of social behaviour, and we matched prominent marks to heterospecific associations.

Baleen whales feed by skimming and gulping plankton, toothed whales by herding prey, sometimes by releasing bubbles, and killer whales by tearing pieces from prey. Some authors have related contrasting marks on specific areas of the body to aspects of feeding behaviour. For example, white flanks might help to herd prey (Wursig and Wursig 1980); white lips might attract squid to the whale's mouth (Gaskin 1967); white flippers or white chins might be used to corral schooling fish and krill (Brodie 1977). For instance, the asymmetrical anterior colouration on the fin whale *Balaenoptera physalus* and dwarf minke whale *Balaenoptera acutorostrata* where the right but not the left side of the lower jaw is white has been considered as an adaptation for startling prey and so driving them into higher concentrations if the whale turns in one direction (but see Tershy and Wiley 1992). A final idea is that eye masks may reduce glare from the sun (Mitchell 1970). We tested whether prominent marks were found in species with particular sorts of diet.

Methods

KB principally used Reeves et al. (2002) and Shirihai and Jarrett (2006) to score colouration in whales, dolphins and porpoises, as well as Harrison and Bryden (1998), Carwardine (2002) and Nowak (2003), and confirmed categorizations using photographs in Google Image. We tried to avoid artists' drawings and photographs of dead specimens wherever possible in favour of colour photographs of live animals. We did not use early descriptions of colouration patterns because they were overly detailed and covered only a small percentage of the clade (Mitchell 1970; Perrin 1972). We disregarded geographic variation in colouration although it can be considerable in this taxon and simply used the most common phenotype (e.g., Rosenbaum et al. 1995; Herzing 1997; Wang et al. 2008). We also disregarded juvenile colouration (Robineau 1984; Jefferson et al. 1997) and instead focused our attention only on adults. We described adult colouration patterns of each of 84 species (data in two out of 86 were missing) using nine simple categorical (and mostly binomial) variables that allowed us to examine hypotheses for cetacean colouration (Table 1). Ecological and behavioural variables were taken from Hoelzel (2002), Mann et al. (2000), Reeves et al. (2002), Nowak (2003), Macdonald (2006), Shirihai and Jarrett (2006) and Perrin et al. (2009), and are described in Table 2 (see also Appendix 1 supplementary material).

We used the phylogeny of Steeman et al. (2009) and where necessary changed names in their tree to conform to Wilson and Reeder (2005). We ran phylogenetically controlled analyses because there was a phylogenetic signal in many of the dependent and independent variables. Because most characteristics of interest were categorical in nature (i.e.,

Table 1 Colouration variables used in this study

Variable	Definition	Scoring
Uniform	90–100% the same colour	0 = not uniform, 1 = uniform, 2 = spotted
Spotted or speckled	Must be fairly distinctive	See above
Countershaded	Dark dorsum and light ventrum covering at least two thirds of the underside (If there is a lot of white or light colour on the sides [e.g., Southern right whale dolphin] or asymmetric colouration, not scored as countershaded). Smooth denotes an intermediate colour transitioning the change from dark to light	0 = not countershaded, 1 = smooth countershaded, 2 = sharp countershaded
Distinctive mark	Colour patch that stands out somewhere on the body	0 = no, 1 = yes
White head	White head cap or lips or chin (chin must not be a continuation of countershading, needs to be restricted to head)	0 = no, 1 = yes
White dorsum	White saddle or white section on the dorsum	0 = no, 1 = yes
White fin	Distinctive white patch or mark on the ventral fin	0 = no, 1 = yes
White flank	Contrasting colouration (white or light colour contrasting a distinct dark colour) on more than a third of the lateral surface	0 = no, 1 = yes
Eye stripe	Any distinct singular mark near or behind the eye	0 = no, 1 = yes

Table 2 Ecological and behavioural variables used in this study

Variable	Definition	Scoring
Phenotypic		
Weight	Female mean weight divided into <150 kg, 150–499 kg, 500–4,999 kg, >5,000 kg based on ranking and natural breaks	Low body weight (0–499 kg) = 1, >500 kg = 0
Length	Female mean length divided into <2.9 m, 3–4.9 m, 5–9.9 m, >10 m based on ranking and natural breaks	Short length (0–4.9 m) = 1 > 5 m = 0
Geography		
Tropics	Within the tropics	Yes (includes part of the tropics) = 1, does not include = 0
Temperate	North of Tropic of Cancer to Arctic Circle and South of Tropic Of Capricorn to Antarctica	Yes (includes part of these areas) = 1, does not include = 0
River systems	Described as living in rivers	Includes river habitat = 1, does not include = 0
Murky waters	Temperate regions or river systems	Exclusively temperate or exclusively rivers = 1, no = 0
Behaviour		
Group living	Average group size	Solitary (1–3 individuals) = 1, medium (4–10) = 2, large (>10) = 3
Interspecific associations	If not specified, taken as "no"	Yes = 1, no = 0
Mating system	High or medium reproductive skew is polygamous; low skew is not polygamous	Yes = 1, no = 0
Food: fish	Categorized as yes if mentioned	Yes = 1, no = 0
Food: squid	As above	Yes = 1, no = 0
Food: krill	As above	Yes = 1, no = 0
Food: fish or squid	As above	Yes = 1, no = 0
Food: fish or krill	As above	Yes = 1, no = 0
Diving depth	Maximum depth, ranked and examined for natural breaks	Shallow (0–100 m) = 1, medium (101–499 m) = 2, deep (>500 m) = 3
Speed	Maximum speed, ranked and examined for natural breaks	Slow (0–9 km/h) = 1, fast (>10 km/h) = 2
Synchronous	Up to 10 photographs of each species breaching were examined provided >1 individual shown. Percentage of observed individuals fully leaping out of water was scored for each. (Thus if 4 out of 10 were in the air, it would be 40% synchronous). Percentages were averaged across photos to give a species score. Species were ranked and examined for natural breaks	Yes (>40% average) = 1, no (<40% average) = 0
Demonstrative behaviour	Breaching, jumping, tail slapping, lobtailing all yes, boat bow riding no. If says occasionally, rarely, or less than other species, it falls in the "no" category, unless it's a very demonstrative such as aerobatic behaviour which would constitute "yes"	Yes = 1, no = 0.

presence vs. absence), TS ran phylogenetically corrected comparative tests using Pagel's (1994) tests for correlated changes to account for shared ancestry using Mesquite 2.72 (Maddison and Maddison 2010) with $\alpha = 0.10$. This procedure tests the independent evolution of two binary characters where observed likelihood ratios are calculated from the data and tested using Monte Carlo simulations using simulated data. The null hypothesis is that the two characters evolved independently, with the alternative being that they evolved together in a correlated fashion. Mesquite calculates the ratio of likelihoods of two models: an 8-parameter model where the rates of change of one character depend on the states of the other and a 4-paramter model where the rates of change are independent for each character. The test then measures the significance of the ratio (log likelihood difference (LD) between the 8 and 4 parameter model) by comparing it to simulated data (10,000 simulations using 10 extra iterations per simulation). In cases where data were missing for one or more species for a given variable, those species with missing data were pruned from the tree for that particular test. We set α at 0.10 because our variables were coarse—for instance species swimming at slow or fast speeds could have been assigned to the wrong category or could obscure interspecific variation. Nonetheless, results of marginal significance ($0.1 > P > 0.05$) are presented only for reference and are not discussed further.

Results

Background matching

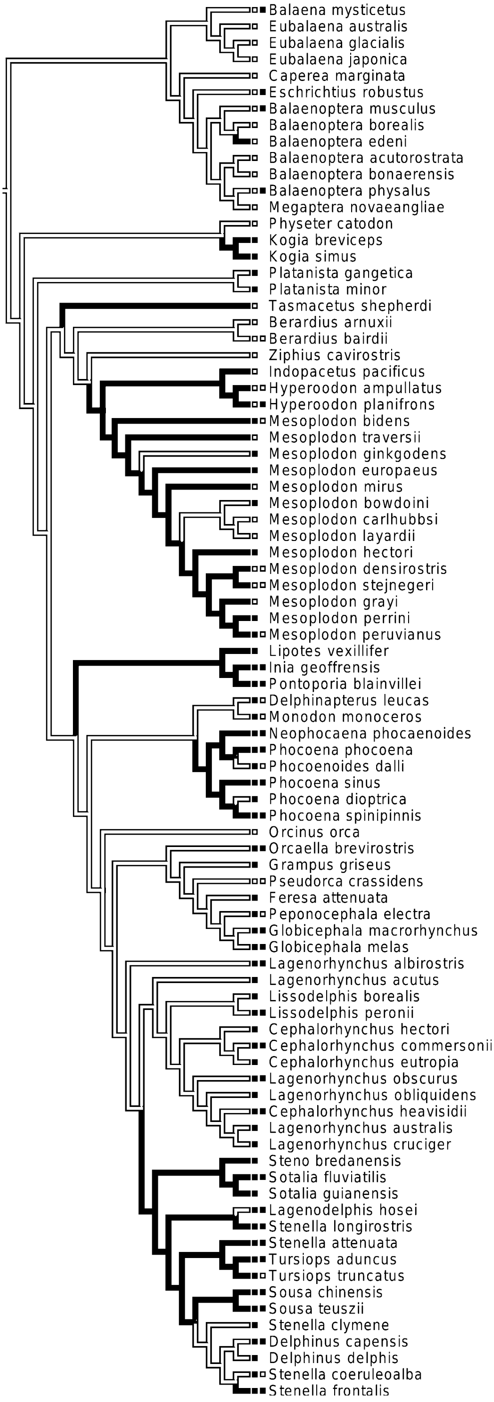
We found no evidence for background matching in cetaceans. There were no significant associations between species that were uniform in colour and species living in low light environments as approximated by those diving to depths of >500 m where there is little penetration of surface light (log likelihood difference$_{(8\text{par}-4\text{par})}$ (LD) 1.58775, $P = 0.3167$, 41 species, or LD = 0.64052, $P = 0.5517$, 40 species dropping belugas *Delphinapterus leucas* as they are white), or with species living in rivers or temperate seas that lack clarity (LD = 1.4042, $P = 0.5611$, 83 species). Spotted cetaceans were no more likely to eat fish or squid prey than other species (LD = 1.00808, $P = 0.1806$, 83 species) suggesting that this sort of colouration was not camouflage against prey with keen vision.

Countershading

We separated countershaded species into those with smooth and sharp gradations because sharp boundaries are easier to see at a distance and so might have different functions. Smoothly countershaded cetaceans (versus all other species, here and below) were slightly more likely to be found in well-lit environments as determined from shallow dives (<100 m) (LD = 3.49207, $P = 0.0894$, 41 species [examine the right hand boxes in Fig. 1]). If countershading was a form of crypsis to avoid predation, it might be expected in smaller species that have a greater range of predators. This idea was supported because smooth countershading was associated with species weighing <500 kg (LD = 4.86143, $P = 0.0265$, 81 species) and with species that were relatively short in length (<5 m) (LD = 5.37405, $P = 0.0199$, 84 species, [Fig. 1, left hand boxes]). Nevertheless, smoothly countershaded cetaceans were, in addition, likely to be those species that feed on fish and squid prey suggesting crypsis against visual prey (LD = 4.23582, $P = 0.0159$, 83 species).

These results generally held for sharply countershaded species also. Whereas there was no significant association with shallow diving (LD = 0.39941, $P = 0.6898$, 41 species),

Fig. 1 Phylogenetic tree of the cetaceans used in this study. Branch colouration signifies the presence (*black*) or absence (*white*) of smooth countershading. The left most set of boxes indicates species of short body length (*filled boxes*), whereas the right most set of *boxes* shows species that dive only to shallow depths (*filled boxes*)



sharply countershaded species (versus all other species) were light in weight (LD = 3.83762, $P = 0.0177$, 81 species) and short in length (LD = 4.97158, $P = 0.0064$, 84 species). They were characteristic of species eating fish or squid prey (LD = 2.43318, $P = 0.0381$, 83 species).

Disruptive colouration

There was little evidence for disruptive colouration being a form of crypsis in well-lit environments. Although there was a slight tendency for species with distinctive markings (a colour patch that stands out somewhere on the body, see Table 2) to be found in tropical seas, often noted for their clarity (LD = 3.76318, $P = 0.0931$; 83 species), species that were sharply countershaded (a possible mechanism for breaking up the body's outline [Rowland 2009]) were not found more often in tropical seas (LD = 0.91882, $P = 0.9139$, 83 species). Nor were distinctively marked (LD = 0.93760, $P = 0.4268$; 41 species) or sharply countershaded species more likely to be shallow divers (see paragraph above).

There was a slight hint that species with white dorsa live in well-lit environments as judged by shallow diving (LD = 1.66487, $P = 0.0984$, 41 species) but this was not the case for species that have stripes running through their eyes (LD = 2.14208, $P = 0.1260$, 41 species).

Communication

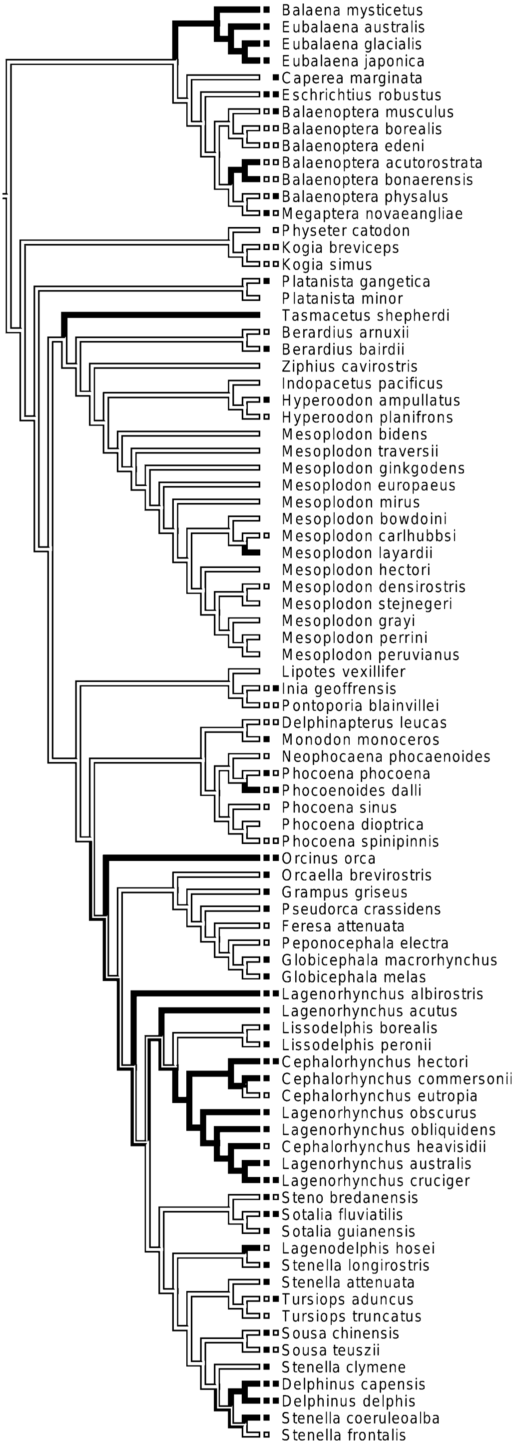
Striking markings seem to be involved in intraspecific communication although not in interspecific communication. Sharply countershaded species were more likely to live in medium sized or large groups (≥ 4 individuals) (LD = 3.10454, $P = 0.0378$, 78 species), although this was not true for species with distinctive marks (LD = 1.47203, $P = 0.4225$, 78 species). Sharply countershaded species showed a slight tendency to exhibit synchronous leaping behaviour (LD = 2.30586, $P = 0.0805$, 41 species). Distinctively marked species and swimming rapidly were tightly associated (LD = 3.62864, $P = 0.0268$, 29 species [Fig. 2 right hand boxes]), although distinctive marks and extent of synchronous breaching were not significantly associated (LD = 2.13081, $P = 0.1560$, 41 species). There was weak evidence that both sorts of species showed demonstrative behaviour above the surface more than would be expected by chance (sharply countershaded species, LD = 3.14477, $P = 0.0618$; having a distinctive mark, LD = 4.20258, $P = 0.0521$ [Fig. 2, left hand boxes], 65 species in both cases) but both fell just short of significance. In particular, species with white flanks showed demonstrative behaviour (LD = 4.25887, $P = 0.0214$, 65 species). White heads (our crude approximation of species with white lower mandibles) did not seem to be involved in sexual selection as they were not found especially in strongly polygynous species (LD = 0.32655, $P = 0.7538$, 21 species); moreover white mandibles is not a sexually dichromatic trait as might be expected under sexual selection.

Sharply countershaded species or those with distinctive marks were not found to associate with other species more than expected by chance (respectively LD = 1.28606, $P = 0.1179$; LD = 1.74282, $P = 0.1224$, 84 species in both cases).

Causing prey to become confused

There was some evidence that some striking markings are involved in prey capture. First, sharply countershaded species and perhaps also species with distinctive marks were those

Fig. 2 Phylogenetic tree of the cetaceans used in this study. Branch colouration signifies the presence (*black*) or absence (*white*) of distinctive marks based on maximum parsimony. The left most set of boxes indicates that the species shows demonstrative behaviour at the surface (*filled boxes*), whereas the right most set of *boxes* shows species that swim at fast speeds (*filled boxes*)



species that capture fish or squid prey (respectively LD = 2.43318, $P = 0.0423$; LD = 2.16277, $P = 0.0862$, 83 species in both cases). More specifically, white flanks were associated with eating fish prey (LD = 4.87520, $P = 0.0230$, 83 species); although white fins were not significant (LD = 2.96002, $P = 0.1069$, 83 species). Having a white head was strongly associated with eating fish or krill prey (LD = 5.07681, $P = 0.0078$, 83 species). There was no support for species with white lips feeding on squid prey (LD = 1.71842, $P = 0.4184$, 83 species), however. Extraordinarily, we found that species with asymmetrical colouration on their lower mandibles were significantly more likely to be species that eat fish or squid (LD = 5.74734, $P = 0.0005$, 83 species).

Miscellaneous

Distinctive markings were somewhat associated with species being of low body weight (LD = 3.15409, $P = 0.0600$, 81 species) possibly hinting at a predator confusion idea. We could find no way to test the idea that hourglass or complex patterns on the flanks of cetaceans serve to hide young and vulnerable calves swimming next to them.

Discussion

We found that countershading is a mechanism by which smaller cetacean species may avoid being seen by their prey; that prominent markings are associated with group living, fast swimming, and ostentatious (demonstrative) behaviour at the surface, suggesting that they function in intraspecific communication; and that white markings on several parts of the body seem to be involved in the capture of fish, squid, and krill. A number of caveats must be made before considering these comparative findings, however. First, and most problematic, the quality of the ecological and behavioural data is poor for many species. Measures that particularly concerned us were extent of polygyny, interspecific associations, and synchronous breaching—the last because we suspect that photographs posted on Google Image would be biased towards photographs of several individual dolphins or porpoises clearing the water simultaneously. In addition we worried that maximum diving depths may not represent the proportion of time that species spend in different parts of the water column. Second, we forced categorizations on some continuous variables looking for natural breaks in the distribution but not always finding them—instead we took the median or subtle breaks in that region of the distribution. For example, length and weights for the great whales are very large but we made the cut-off between large and small species at 5 m and 500 kg, far smaller than that of the great whales. Dichotomization of these variables masks potentially important variation between species although data for some species are poorly known. Third, we are concerned that some of the variables do not provide a strong test of specific hypotheses. For example, tropical waters may not be an approximation for well illuminated seas. That said, we know of no better data to which to turn. We are far more confident of our measures of colouration because our variables and categories were coarse and hence easy to score; in those relatively few species in which we noted intraspecific variation, TC and KB resolved categorizations through consensus. Finally, it is worth noting that cetacean phylogenetics is an active field of enquiry, and there is debate about a number of species classifications. Future changes to the cetacean tree might alter our findings, especially those on the cusp of statistical significance and there are a number of these.

Countershading in cetaceans may be a form of concealment from prey because it is seen in small cetaceans (for both smooth and sharp countershaded) and small cetaceans take fish or squid prey (LD $= 2.66850$, $P < 0.0001$, 80 species), and indeed this form of colouration is directly associated with eating fish or squid. These results query predictions derived from modeling that indicate no differences in visibility of light and dark ventral surfaces when viewed from below (Johnsen 2002). The link between sharp countershading and a diet of fish and squid is similar to findings from another taxon—seabird species feeding in the mid-water column are more likely to be countershaded than surface or bottom feeders (Cairns 1986; Bretagnolle 1993) although birds will principally approach prey from above whereas cetaceans may approach from several directions.

We suspect that while smooth countershading and sharp countershading may serve similar functions in cetaceans as both are associated with being small in size, sharp countershading is additionally associated with a number of variables indicative of intraspecific communication (see below). We cannot, however, discount the idea that sharp countershading may also be a form of crypsis perhaps as a means of background matching with the dark dorsal surface blending in with the dark depths beneath, and the light ventrum blending in with the light surface waters above (Beddard 1895; Kiltie 1988; Ruxton et al. 2004). In sum, countershading seems to be the principal mechanism of crypsis in cetaceans probably as camouflage when approaching prey, whereas sharp countershading may additionally function as a distinctive mark that is involved in intraspecific communication.

Second, we found that certain prominent forms of colouration are apparently involved in intraspecific communication as judged by relationships between sharply countershaded species and living in groups, and also by distinctive markings and swimming rapidly. This has a parallel with artiodactyls where species with white tails tend to be social (Stoner et al. 2003b). Prominent colouration could be involved in group members keeping in contact with each other over short ranges, especially when traveling fast (Weihs 2004; Connor et al. 2006). Striking markings, especially white flanks, were associated with species that exhibit showy activity at the surface such as breaching and lobtailing. Indeed, humpback whales *Megaptera novaeangliae* are noted for slapping their long white flippers against the surface (Clapham 2000). Striking markings may enable individuals to coordinate their high speeds underwater if they can see each other clearly—which could result in synchronous leaping. Third, we noted that a number of different forms of striking marks—white heads, white flanks, perhaps white flippers, and even asymmetrical white lower mandibles—were associated with eating fish, squid and krill. These white patches may serve to disorient prey or force a school together allowing prey to be captured more easily by cetacean predators (Watkins & Schevill 1979; Wilson et al. 1987; Wursig et al. 1990). There was a general association between colouration asymmetry and feeding on fish or squid prey. However, asymmetrical colouration is limited to just two whale species and the comparative approach has limited power in these circumstances; observations do not suggest that fin whales lunge at prey in an asymmetrical fashion (Tershy and Wiley 1992); and the mechanism is by which such colouration might facilitate feeding is not clear, so we are suspicious of this finding. More generally, our data show that prominent colouration may be related to certain diets and feeding behaviour and actually be of general significance in cetaceans. Such a function for colouration has not been proposed or found in terrestrial mammals (Caro 2005, 2009) although it has in birds (e.g., Jabonski et al. 2006).

Other than through countershading, there was little support for cetacean colouration being an adaptation for camouflage. Our tests of both background matching and disruptive colouration fell far short of significance. On reflection, this is not such a surprising finding given that selection on colouration may be lessened in depths where little light penetrates and that the large body sizes of many whale species make them relatively safe from predators—the main extant predators of most adult whales are only killer whales that primarily sense their environment acoustically. Our efforts here set out to test all the hypotheses for whale, dolphin and porpoise colouration put forward in the literature and it is worth noting that sexual signaling, and interspecific communication with other species, discussed for some delphinid species, were not supported by our tests.

Clearly, colouration in cetaceans appears to be driven by several evolutionary forces, namely crypsis through countershading, communication with conspecifics—perhaps promoting group cohesion—and the necessity to disorient and corral prey. Our findings must be treated as preliminary, however, because the data are coarse, but they do extend our understanding of cetacean colouration. Now it remains to be seen whether these findings about the evolution of colouration in this clade hold true for other marine taxa.

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Supplementary material 1 (XLS 59 kb). Appendix 1. Variables used in this study; see Tables 1 and 2 for meaning of numbers in the body of the appendix, – denotes missing data. Column headings: UorS, uniform or spotted; CS, countershaded; DM, distinctive mark; WH, white head; WD, white dorsum; WF, white ventral fin; Wfl, white flank, ES, eye stripe; Tr, tropical waters; Te, temperate waters; MW, murky waters; Group, group size; Inter, interspecific associations; Food, main food type (F: fish, S: squid, K: krill); Poly, polygamous; D, depth; S, speed; SB, synchronous behaviour; DM, Demonstrative behaviour; * *Balaenoptera edeni* or *B. brydei*

Species Name	**Common Name**	**UorS**	**CS**	**DM**	**WH**	**WD**	**WF**	**WFl**	**ES**	**Weight**	**Length**	**Tr**	**Te**	**MW**	**Group**	**Inter**	**Poly**	**Food**	**D**	**S**	**SB**	**DB**
Balaena mysticetus	Bowhead Whale	1	0	1	1	0	0	0	0	>5,000	>10	0	0	0	2	0	0	K, F or K	2	-	-	1
Eubalaena australis	Southern Right Whale	0	0	1	0	0	0	0	0	>5,000	>10	0	1	0	1	0	0	K, F or K	-	-	-	1
Eubalaena glacialis	North Atlantic Right Whale	0	0	1	0	0	0	0	0	>5,000	>10	0	1	0	1	0	0	none	-	-	1	1
Eubalaena japonica	North Pacific Right Whale	0	0	1	0	0	0	0	0	>5,000	>10	0	1	0	1	0	0	none	-	-	-	1
Balaenoptera acutorostrata	Common Minke Whale	0	2	1	0	0	1	0	0	>5,000	<10	0	1	1	1	0	-	F, S, F or S, F or K	-	1	1	0
Balaenoptera bonaerensis	Antarctic Minke Whale	0	2	1	0	0	1	0	0	>5,000	<10	1	1	0	1	0	-	K, F or K	-	1	1	0
Balaenoptera borealis	Sei Whale	0	2	0	0	0	0	0	0	>5,000	>10	1	1	0	1	0	-	F, S, F or S, F or K	-	1	1	0
Balaenoptera edeni *	Bryde's Whale	0	1	0	0	0	0	0	0	>5,000	>10	1	1	0	1	0	-	F, F or S, F or K	-	1	-	0
Balaenoptera musculus	Blue Whale	1	0	0	0	0	0	0	0	>5,000	>10	1	1	0	1	0	-	K, F or K	1	2	-	0
Balaenoptera physalus	Fin Whale	0	2	0	0	0	1	0	0	>5,000	>10	1	1	0	2	0	-	F, K, F or S, F or K	2	2	-	0
Megaptera novaeangliae	Humpback Whale	0	0	0	0	0	1	1	0	>5,000	>10	1	1	0	1	0	0	F, K, F or S, F or K	-	1	0	1
Eschrichtius robustus	Gray Whale	2	0	0	0	0	0	0	0	>5,000	>10	0	1	1	1	0	0	none	1	2	0	1
Caperea marginata	Pygmy Right Whale	0	2	0	0	0	1	0	0	<5,000	<10	0	1	0	1	0	-	K, F or K	-	2	-	-
Cephalorhyncus commerso	Commerson's Dolphin	0	2	1	0	1	0	1	0	<150	<3	0	1	1	2	1	-	, S, K, F or S, F or K	1	-	1	1
Cephalorhyncus eutropia	Chilean Dolphin	0	2	0	0	0	0	1	0	<150	<3	0	1	1	1	0	-	F, S, F or S, F or K	-	-	0	0
Cephalorhyncus heavisidii	Heaviside's Dolphin	0	0	1	0	0	0	1	0	<150	<3	0	1	1	2	0	-	F, S, F or S, F or K	1	-	1	0
Cephalorhyncus hectori	Hector's Dolphin	0	0	1	0	0	0	1	0	<150	<3	0	1	1	2	0	-	F, S, F or S, F or K	-	2	0	1
Delphinus capensis	Long-beaked Common Dolphin	0	0	1	0	0	0	1	0	<150	<3	1	1	0	3	0	-	, S, K, F or S, F or K	1	2	0	1
Delphinus delphis	Short-beaked Common Dolphin	0	0	1	0	0	0	1	0	<150	<3	1	1	0	3	0	1	, S, K, F or S, F or K	-	2	1	1
Delphinus tropicalis	Arabian Common Dolphin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F, S, F or S, F or K	-	-	-	-
Feresa attenuata	Pygmy Killer Whale	1	0	0	1	0	0	0	0	<150	<3	1	0	0	3	0	-	F, S, F or S, F or K	-	-	-	0
Globicephala macrorhyncus	Short-finned Pilot Whale	0	0	0	0	0	0	0	1	<5,000	<5	1	1	0	3	1	1	S, F or S	1	-	-	1
Globicephala melas	Long-finned Pilot Whale	0	0	0	0	0	0	0	1	<5,000	<5	0	1	0	3	1	1	F, S, F or S, F or K	1	-	0	1
Grampus griseus	Risso's Dolphin	0	0	0	0	0	0	0	0	<500	<5	1	1	0	3	1	-	S, F or S	-	-	1	1
Lagenodelphis hosei	Fraser's Dolphin	0	2	1	0	0	0	1	0	<500	<3	1	1	0	3	1	1	F, S, F or S, F or K	2	-	0	0
Lagenorhynchus acutus	Atlantic White-sided Dolphin	0	0	1	0	0	0	1	0	<500	<3	0	1	0	3	1	-	F, S, F or S, F or K	-	-	0	1
Lagenorhynchus albirostris	White-beaked Dolphin	0	0	1	0	1	0	1	0	<500	<3	0	1	0	2	1	-	F, S, F or S, F or K	1	2	0	1
Lagenorhynchus australis	Peale's Dolphin	0	0	1	0	0	0	1	0	<150	<3	0	1	1	2	1	-	F, S, F or S, F or K	-	-	0	1
Lagenorhynchus cruciger	Hourglass Dolphin	0	0	1	0	0	0	1	0	<150	<3	0	1	0	2	1	-	F, S, F or S, F or K	-	2	1	1
Lagenorhynchus obliquiden	Pacific White-sided Dolphin	0	0	1	0	1	0	1	0	<150	<3	0	1	1	3	1	-	F, S, F or S, F or K	-	-	1	1
Lagenorhynchus obscurus	Dusky Dolphin	0	0	1	0	0	0	1	0	<150	<3	0	1	0	3	1	0	, S, K, F or S, F or K	2	-	1	1
Lissodelphis borealis	Northern Right Whale Dolphin	0	2	0	0	0	0	0	0	<150	<3	0	1	1	3	1	-	F, S, F or S, F or K	-	-	1	1
Lissodelphis peronii	Southern Right Whale Dolphin	0	0	0	0	0	1	1	0	<150	<3	0	1	1	3	1	-	, S, K, F or S, F or K	2	-	1	1
Orcaella brevirostris	Irrawaddy Dolphin	0	0	0	0	0	0	0	0	<150	<3	1	0	0	2	0	-	F, S, F or S, F or K	1	-	0	1
Orcinus orca	Killer Whale	1	0	1	1	1	0	1	1	>5,000	<10	1	1	0	2	0	1	F, S, F or S, F or K	-	2	0	1
Peponocephala electra	Melon-headed Whale	1	0	0	1	0	0	0	0	<500	<3	1	0	0	3	1	-	F, S, F or S, F or K	3	-	0	0
Pseudorca crassidens	False Killer Whale	1	0	0	0	0	0	0	0	<5,000	<10	1	1	0	3	1	-	F, S, F or S, F or K	3	-	0	1
Sotalia guianensis	Costero	0	1	0	0	0	0	0	0	-	<3	1	1	0	3	0	-	F, F or S, F or K	-	-	1	1
Sotalia fluviatilis	Tucuxi	0	1	0	0	0	0	0	0	<150	<3	0	0	1	2	0	1	F, F or S, F or K	1	2	0	1
Sousa chinensis	Indo-Pacific Hump-backed Dolphin	0	1	0	0	0	0	0	0	<500	<3	1	1	0	2	1	-	F, S, F or S, F or K	1	1	0	1
Sousa teuszii	Atlantic Hump-baked Dolphin	0	1	0	0	0	0	0	0	<500	<3	1	1	0	2	1	-	F, S, F or S, F or K	1	1	1	1
Stenella attenuata	Pantropical Spotted Dolphin	0	1	0	0	0	0	0	0	<150	<3	1	1	0	3	0	0	F, S, F or S, F or K	1	-	1	1
Stenella clymene	Clymene Dolphin	0	2	0	0	0	0	1	0	<150	<3	1	1	0	3	1	-	F, S, F or S, F or K	-	-	1	1
Stenella coeruleoalba	Striped Dolphin	0	2	1	0	0	0	1	0	<150	<3	1	1	0	3	0	-	F, S, F or S, F or K	3	-	1	1
Stenella frontalis	Atlantic Spotted Dolphin	2	1	0	0	0	0	0	0	<150	<3	1	1	0	2	0	-	F, S, F or S, F or K	2	-	1	0
Stenella longirostris	Spinner Dolphin	1	1	0	0	0	0	1	0	<150	<3	1	1	0	3	1	1	F, F or S, F or K	2	-	0	1
Steno bredanensis	Rough-toothed Dolphin	0	1	0	0	0	0	0	0	<150	<3	1	1	0	3	1	-	F, S, F or S, F or K	-	1	0	1
Tursiops aduncus	Indio-Pacific Bottlenose Dolphin	0	1	0	0	0	0	0	0	<500	<3	1	1	0	2	1	1	F, S, F or S, F or K	2	2	1	0
Tursiops truncatus	Common Bottlenose Dolphin	0	1	0	0	0	0	0	0	<500	<5	1	1	0	2	1	1	F, K, F or S, F or K	3	-	-	0
Delphinapterus leucas	Beluga	1	0	0	0	0	0	1	0	<5,000	<5	0	0	0	3	0	-	F, S, F or S, F or K	3	1	-	0
Monodon monoceros	Narwhal	0	0	0	0	0	0	1	0	<5,000	<5	0	0	0	3	0	1	F, S, F or S, F or K	3	-	0	1
Neophocaena phocaenoides	Finless Porpoise	0	1	0	0	0	0	0	0	<150	<3	1	1	0	1	0	-	F, S, F or S, F or K	1	-	-	0
Phocoena dioptrica	Spectacled Porpoise	0	2	0	0	0	1	1	0	<150	<3	0	1	1	1	0	-	, S, K, F or S, F or K	-	-	-	-
Phocoena phocaena	Harbor Porpoise	0	1	0	0	0	0	1	0	<150	<3	0	1	0	2	0	0	F, S, F or S, F or K	2	1	-	1
Phocoena sinus	Vaquita	0	1	0	0	0	0	0	1	<150	<3	0	1	1	1	0	-	F, S, F or S, F or K	1	-	-	0

Species Name	Common Name	UorS	CS	DM	WH	WD	WF	WFl	ES	Weight	Length	Tr	Te	MW	Group	Inter	Poly	Food	D	S	SB	DB
Phocoena spinipinnis	Burmeister's Porpoise	0	1	0	0	0	0	0	0	<150	<3	0	1	1	1	0	-	F, K, F or S, F or K	1	1	-	0
Phocoenoides dalli	Dall's Porpoise	0	0	1	0	0	0	1	0	<500	<3	0	1	1	2	0	1	F, S, F or S, F or K	3	2	-	0
Kogia breviceps	Pygmy Sperm Whale	0	1	0	0	0	0	0	0	<500	<5	1	1	0	2	0	-	F, S, F or S, F or K	-	1	-	0
Kogia sima	Dwarf Sperm Whale	0	1	0	0	0	0	0	0	<500	<3	1	1	0	2	0	-	F, S, F or S, F or K	-	1	-	0
Physeter catodon	Sperm Whale	1	0	0	1	0	0	0	0	>5,000	>10	1	1	0	3	0	-	S, F or S	-	1	-	-
Platanista gangetica	Ganges River Dolphin	1	0	0	0	0	0	0	0	<150	<3	0	0	1	1	0	-	F, F or S, F or K	-	-	-	1
Platanista minor	Indus River Dolphin	1	0	0	0	0	0	0	0	<150	<3	0	0	1	1	0	-	F, F or S, F or K	-	-	-	-
Inia geoffrensis	Amazon River Dolphin	0	1	0	0	0	0	0	0	<150	<3	0	0	1	1	0	-	F, F or S, F or K	1	2	-	0
Lipotes vexillifer	Baiji	0	1	0	0	0	0	0	0	<500	<3	0	0	1	2	0	-	F, F or S, F or K	-	-	-	-
Pontoporia blainvillei	Franciscana	0	1	0	0	0	0	0	0	<150	<3	0	1	0	1	0	-	F, S, F or S, F or K	1	1	-	0
Berardius arnuxii	Arnoux's Beaked Whale	0	0	0	0	0	0	0	0	>5,000	<10	0	1	0	2	0	-	F, S, F or S, F or K	-	-	-	0
Berardius bairdii	Baird's Beaked Whale	2	0	0	0	0	0	0	0	>5,000	>10	0	1	1	3	0	-	F, S, F or S, F or K	3	-	0	1
Hyperoodon ampullatus	Northern Bottlenose Whale	0	1	0	0	0	0	0	1	>5,000	<10	0	1	0	2	0	1	F, S, F or S, F or K	3	-	-	1
Hyperoodon planifrons	Southern Bottlenose Whale	0	1	0	0	0	0	0	1	>5,000	<10	0	1	0	2	0	-	F, S, F or S, F or K	2	-	0	0
Indopacetus pacificus	Tropical Bottlenose Whale	0	1	0	0	0	0	0	1	<500	<10	1	1	0	3	0	-	-	-	-	-	-
Mesoplodon bidens	Sowerby's Beaked Whale	0	1	0	0	0	0	0	0	<5,000	<5	0	1	1	2	0	-	F, S, F or S, F or K	3	-	-	-
Mesoplodon bowdoini	Andrew's Beaked Whale	1	0	0	1	0	0	0	0	<5,000	<5	0	1	1	-	0	-	S, F or S	-	-	-	-
Mesoplodon carlhubbsi	Hubb's Beaked Whale	1	0	0	1	0	0	0	0	<5,000	<10	0	1	0	1	0	-	F, S, F or S, F or K	-	-	-	0
Mesoplodon densirostris	Blainville's Beaked Whale	0	1	0	0	0	0	0	0	<5,000	<10	1	1	0	2	0	-	F, S, F or S, F or K	3	-	-	0
Mesoplodon europaeus	Gervais' Beaked Whale	0	1	0	0	0	0	0	1	<5,000	<5	1	1	0	2	0	-	S, F or S	-	-	-	-
Mesoplodon ginkgodens	Ginkgo-toothed Beaked Whale	1	0	0	0	0	0	0	0	<5,000	<5	1	1	0	-	0	-	F, S, F or S, F or K	-	-	-	-
Mesoplodon grayi	Gray's Beaked Whale	0	1	0	1	0	0	0	0	<5,000	<10	0	1	1	2	0	-	F, S, F or S, F or K	-	-	-	-
Mesoplodon hectori	Hector's Beaked Whale	0	1	0	1	0	0	1	0	<5,000	<5	0	1	1	-	0	-	S, F or S	-	-	-	-
Mesoplodon layerdii	Strap-toothed Whale	0	0	1	1	1	0	1	0	<5,000	<10	0	1	1	1	0	-	S, F or S	-	-	-	-
Mesoplodon mirus	True's Beaked Whale	0	1	0	0	0	0	1	1	<5,000	<10	0	1	0	-	0	-	F, S, F or S, F or K	-	-	-	-
Mesoplodon perrini	Perrin's Beaked Whale	0	1	0	0	0	0	0	1	-	<5	-	-	-	-	0	-	S, F or S	-	-	-	-
Mesoplodon peruvianus	Pygmy Beaked Whale	0	1	0	0	0	0	1	1	-	<5	1	1	0	1	0	-	F, S, F or S, F or K	3	-	-	-
Mesoplodon stejnegeri	Stejneger's Beaked Whale	0	1	0	1	0	0	0	0	<5,000	<10	0	1	1	1	0	-	S, F or S	3	-	-	-
Mesoplodon traversii	Spade-toothed Whale	-	-	-	-	-	-	-	-	-	<10	-	-	-	-	0	-	-	-	-	-	-
Tasmacetus shepherdi	Shepherd's Beaked Whale	0	1	1	0	0	0	1	0	<5,000	<10	0	1	1	-	0	-	F, S, F or S, F or K	-	-	-	-
Ziphius cavirostris	Cuvier's Beaked Whale	1	0	0	1	0	0	0	0	<5,000	<10	1	1	0	2	0	-	F, S, F or S, F or K	-	-	-	-