Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales?

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Prey availability and predation risk are important determinants of habitat use, but their importance may vary across spatial scales. In many marine systems, predator and prey distributions covary at large spatial scales, but do no coincide at small spatial scales. We investigated the influences of prey abundance and tiger shark (*Galeocerdo cuvier*) predation risk on Indian Ocean bottlenose dolphin (*Tursiops aduncus*) habitat use across multiple spatial scales, in Shark Bay, Western Australia. Dolphins were distributed between deep and shallow habitats and across microhabitats within patches approximately proportional to prey density when shark abundance was low. When shark abundance was high, foraging dolphins greatly reduced their use of dangerous, but productive, shallow patches relative to safer deep ones. Also, dolphins reduced their use of interior portions of shallow patches relative to their edges, which have higher predator density but lower intrinsic risk (i.e. a higher probability of escape in an encounter situation). These results suggest that predation risk and prey availability influence dolphin habitat use at multiple spatial scales, but intrinsic habitat risk, and not just predator encounter rate, is important in shaping dolphin space use decisions. Therefore, studies of habitat use at multiple spatial scales can benefit from integrating data on prey availability and the subcomponents of predation risk.

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Identifying factors that influence habitat selection at multiple spatial scales is of considerable importance in ecology, and both food availability and predation risk are likely to influence distribution patterns across scales. In general, predators should attempt to match the distribution of their prey, and prey to avoid areas of high predation risk (reviewed by Lima and Dill 1990, Lima 1998). The result of such predator–prey games is that the distribution of predators relative to their prey may be dynamic and matches between distributions may depend heavily on the spatial scale being investigated.

Many studies, especially in marine habitats, have shown poor matches between distributions of predators and their prey at relatively small spatial scales (Sih 1984, Russell et al. 1992, Mehlum et al. 1999, Fauchald et al. 2000, Guinet et al. 2001). These mismatches in distributions can be caused by the inability of marine predators to predict the distribution of their prey and anti-predator behavior of mobile prey species. At relatively large spatial scales, prey distributions tend to be predictable and anti-predator behavior is unlikely to result in disjunct distributions, while prey abundances tend to be less predictable and antipredator behavior more important at small spatial scales. For example, common murres (*Uria aalge*) and shearwaters (*Puffinus griseus* and *P. tenuirostris*) match the distribution of their fish

prey at the scale of hundreds of kilometers but not at the scale of kilometers, which may be due to fish diving to escape seabird predation (Logerwell and Hargreaves 1996). When prey abundance is predictable at smaller spatial scales, predators may match prey distributions at these scales. Habitat heterogeneity may enhance the predictability of resources. For example, seabirds foraging in areas of stable upwelling close to their breeding sites in the northeastern Pacific showed a strong match to their prey distributions at fine spatial scales (Parrish et al. 1998), and pied cormorants (*Phalacrocorax varius*) match the distribution of their fish prey at the scale of tens of meters in the heterogeneous seagrass and sand habitats of a tropical embayment in Australia (Heithaus 2005).

Deviations from animal distributions predicted by those of their prey also may be influenced by predation risk since many foragers must select between foraging in food-rich habitats that are more dangerous and habitats that are safer but have lower prey abundance (Lima and Dill 1990, Lima 1998). In such situations, foragers in dangerous habitats often are found in lower abundance than predicted by food resources, resulting in a mismatch in distributions of middle predators ("foragers") and their prey.

The risk to foragers within a habitat can be divided into the probability of encountering a predator and intrinsic habitat risk (habitat attributes that modify the conditional probability of prey capture in an encounter situation; Gotcietas and Colgan 1989, Hugie and Dill 1994). Theory predicts that habitat differences in intrinsic risk may result in a mismatch between forager and prey distributions regardless of the distribution of the forager's predator. A model of mobile predators and prey (foragers) selecting one of two habitats that differ in intrinsic habitat risk and forager resources suggests that predators should be distributed proportionate to the food of the forager and foragers should be distributed proportionate to intrinsic risk (Hugie and Dill 1994, Heithaus 2001a). Therefore, unless a forager's prey is most abundant in intrinsically safer habitats, there should not be a positive relationship between forager and prey densities or those of predators and foragers. To our knowledge, no studies have investigated the influence of spatial scale on habitat use in three trophic level predator–prey interactions. Furthermore, few field studies have attempted to identify the component of predation risk (i.e. encounter rate vs intrinsic risk) that is of the greatest importance to prey habitat selection.

Coastal odontocete cetaceans provide an appropriate system for investigating the influence of predation risk and prey availability on habitat use decisions at multiple spatial scales. Many species are at risk from numerous predators, especially large sharks (Heithaus 2001b, 2001c), and they are likely to respond to resources and/or predation risk at multiple spatial scales due to the heterogeneous nature of many habitats and the predictability of prey and predator distributions (Heithaus 2005). Habitat use by Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia is influenced by tiger shark predation risk and the abundance of teleost prey at the scale of deep and shallow patches (1000s of meters, Heithaus and Dill 2002). In general, dolphins are distributed across deep and shallow habitats in proportion to prey resources when sharks are absent but largely abandon foraging in productive shallow habitats when shark abundance increases due to the riskiness of these habitats. Both tiger shark abundance (encounter rate) and the intrinsic risk of predation vary at the microhabitat level (10s to 100s of meters; Heithaus et al. in press) raising the possibility that dolphins also may respond at this spatial scale. The objectives of this study were to 1) determine the responses of dolphins to predation risk and prey availability at the scale of habitat patches and microhabitats within patches, and 2) determine whether predator encounter rate alone influences dolphin habitat use decisions.

Methods

Study site

The study was conducted in the Eastern Gulf of Shark Bay, a large semi-enclosed bay along the central coast of Western Australia (25°45′S, 113°44′E; Heithaus 2001d). At the scale of patches, habitats can be divided into shallow banks (≤ 4.5 m depth), which are largely covered by seagrass, and surrounding deeper waters (generally 6–12 m depth) with primarily sandy bottoms. Shallow banks can be divided into interior and edge microhabitats while deep habitats can be subdivided into open water, with relatively low current velocities, and channels, where currents can exceed 3 km h^{-1}. In this study we define microhabitats as follows: deep channel, deep open water, shallow interior (<2.5 m depth and >75 m from water >4.5 m depth), and shallow edge (waters <2.5 m depth within 75 m of water >4.5 m depth, and waters 2.5–4.5 m depth). Nine sampling zones, representing replicates of these two habitat types, were defined for the purposes of this study and were mapped into a Geographic Information System (GIS, MapInfo Professional version 4.5, MapInfo Corporation; Fig. 1). Zones of similar habitat type (e.g. deep) were all separated by intervening habitat of the other type (e.g. shallow), reducing spatial autocorrelation. All shallow zones contained both edge and interior microhabitats and the less abundant microhabitat represented 35–46% of total zone area. Sampling occurred in five deep zones. Three contained both channel and open microhabitats, while two adjacent zones were
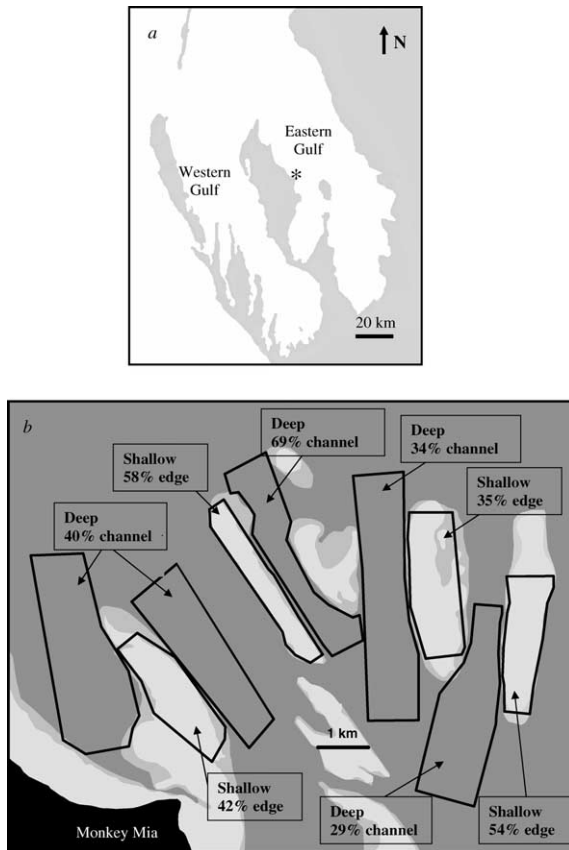
Fig. 1. (a) Study area in Shark Bay, Western Australia. (b) Sampling zones represent replicates of deep and shallow habitat types. All shallow habitats contain both edge and interior microhabitats. Three deep zones contained both channel and open microhabitats and two others that contained only a single microhabitat were combined into a single sampling zone. Proportions of shallow zones that are edge microhabitat and proportions of deep zones that are channel habitat are given inside boxes. The two joined zones are linked to the same box.

composed of a single microhabitat each (one all channel, one all open) and were combined for analyses (Fig. 1). For the resulting four deep zones, the less abundant microhabitat comprised 29–40% of total zone area.

There is considerable variation in the abundance of tiger sharks in the study area, with relatively rapid transitions between seasons with high shark catch rates and very low shark catch rates (Heithaus 2001d). Variation in shark abundance is consistently high from September–May, but sharks may be either present in substantial numbers, or largely absent, from June–August, depending on the year (Heithaus 2001d, Wirsing et al. in press). Therefore, we are able to analyze patterns of dolphin habitat and microhabitat use relative to shark abundance ("present" or "absent") without the confound of seasonal variation in other factors (Heithaus and Dill 2002).

Dolphin habitat and microhabitat use

Dolphin microhabitat use was investigated using belt transects and dolphin group surveys. A transect line, between 2.8 and 4.6 km long, was positioned in the middle of each sample zone and a sighting belt extended 500 m to either side of the transect except where the transect line was within 500 m of another zone or habitat. Three observers drove along the transect in a 4.5 m boat at 6–9 km h^{-1}. To ensure minimal variation in sighting efficiency among days and with distance from the survey vessel, transects were only included in analyses if they were conducted in Beaufort wind conditions of 2 or less, with the majority occurring in Beaufort 0 or 1 conditions. The order and direction in which transects were driven was haphazard to minimize the influence of tidal and diel patterns on these data. A total of 626 transect passes were used in these analyses.

Upon sighting a group of dolphins along a transect, the GPS position on the transect was marked and we departed the transect line to survey the group. Data on group size, composition, and behavior were recorded along with environmental information (cf. Heithaus and Dill 2002 for detailed methods and behavioral classifications). Individual identifications of dolphins were made using distinctive patterns of nicks and cuts to the dorsal fin (Smolker et al. 1992). Once a survey was completed, we returned to the point of departure and resumed driving the transect. GPS locations of all dolphin groups engaged in foraging were mapped into the GIS. Groups outside of sampling zones were omitted from subsequent analyses, and the microhabitat of all those inside zones was determined.

We used ANOVA to determine the effects of shark presence, sampling zone, and their interaction on the relative use of microhabitats within a habitat type during foraging. Analyses were carried out separately for microhabitats within deep and shallow habitats. Shark presence and zone were considered fixed effects and class variables. In order to avoid biases associated with variation in the number of passes along a transect in a season, data on dolphin densities within each zone were collapsed into a single mean proportion of foraging dolphin density in shallow patches relative to deep ones (RD_s), edge microhabitats relative to interior ones (RD_e) for shallow patches, and channel microhabitats relative to open ones (RD_c) for deep patches. Dolphin density was calculated by dividing the number of dolphins sighted within a patch or microhabitat on a transect within a season by the total area of that patch or microhabitat surveyed within the transect. For example, we calculated the relative density of foraging dolphins in edge microhabitat of zone i (RD_{ei}) using

$$RD_{ei} = \frac{d_{ei}}{d_{ei} + d_{ti}}$$

where d_{ei} is the density of dolphins within edge microhabitats of transect i in a particular season and d_{ti} is the density of dolphins within interior microhabitats. All data were arcsin transformed, and non-significant interactions ($P > 0.10$) were removed from analyses. Patch-level data were originally presented in Heithaus and Dill (2002), but have been re-analyzed and presented in the above manner for consistency with microhabitat analyses.

Food abundance

The biomass of dolphin prey (teleosts) was assessed using Antillean-Z fish traps (cf. Heithaus 2004a for a description of trap design). Traps were baited with approximately 250 g of cut pilchards (*Sardinops neopilchardus*) and usually set in at least two, and often three, microhabitat types concurrently. Traps were set for approximately two hours to maximize catch rate and minimize trap saturation (Sheaves 1995). When traps were recovered, the fork length (FL) of each fish was measured and a number of individuals of each species were weighed to generate length-mass relationships (Heithaus 2004a) which were used to determine overall catch biomass. Biomass available to dolphins was calculated using species that dolphins are known to consume. Fish <10 cm FL were removed from biomass calculations since they probably represent a relatively small proportion of dolphin diets (Heithaus and Dill 2002). We used ANOVA on $\log(x+1)$-transformed data to determine the effects of microhabitat, shark presence, and an interaction between these factors on catch biomass. To account for resampling within zones, we tested for heterogeneity among zones of a microhabitat type. Because all sampling zones within each habitat and microhabitat were determined to be similar, they were combined for analysis.

Predation risk

Temporal and spatial variation in the abundance of tiger sharks is based on data collected within the study area during the same period as the dolphin study (Heithaus 2001d, Heithaus et al. 2002, in press). Shark densities were high during four seasons (three Sept–May, one June–Aug) and virtually absent during two seasons (both June–Aug) (Heithaus 2001d). Randomization analyses of acoustic tracks of 41 sharks has revealed that tiger sharks in the study area exhibit a strong preference for shallow habitat patches over deep ones, with mean use of shallow habitats about 1.5 times greater than expected by random habitat choice

(RD$_s$ =0.60; Heithaus et al. 2002). Tracked sharks showed a preference for both shallow microhabitats over both deep ones (Heithaus et al. in press). Within shallow patches, sharks preferred edge microhabitats over interior microhabitats (RD$_e$ =0.60; Heithaus et al. in press), but showed no significant microhabitat preference within deep patches (RD$_c$ =0.47). However, catch rates are slightly higher in open microhabitats than in channels (Heithaus et al. in press).

Results

Fish biomass was significantly influenced by microhabitat ($F_{3,589}$ =33.7, $P < 0.0001$). There was no variation in fish abundance across shallow microhabitats regardless of shark presence (Fig. 2). Both shallow microhabitats had greater biomass than deep microhabitats during both periods (Fig. 2). Deep channel microhabitats had greater biomass than deep open microhabitats, and this pattern did not vary with shark presence (Fig. 2). There was greater biomass caught in traps when sharks were absent than when they were present ($F_{1,589}$ =6.3, $P = 0.012$), but this was driven primarily by changes within deep microhabitats (Fig. 2).

Based on data presented in Heithaus and Dill (2002), there was a significant interaction between shark presence and patch type on the density of foraging dolphins ($F_{1,57}$ =6.8, $P =0.01$) as well as significant main effects of each (shark presence, $F_{1,57}$ =6.6, $P =0.01$; habitat, $F_{1,57}$ =6.5, $P =0.01$). When tiger sharks were absent, foraging dolphins were distributed across deep and shallow patches approximately proportional to relative fish biomass, but there was a shift to using shallow patches less often than expected based on the distribution of fish resources when sharks were present (Fig. 3).
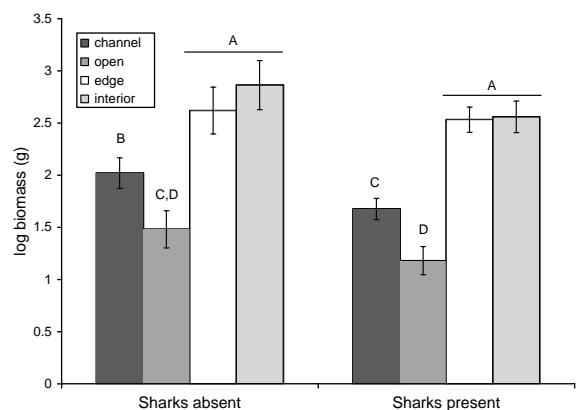

Fig. 2. Mean fish biomass captured by fish traps relative to shark presence and microhabitat. Error bars are ±SE. Bars labeled with the same letter are not significantly different from one another. Note that the interaction between microhabitat and shark presence in not significant ($F_{3,591}$ =0.22, $P =0.88$).
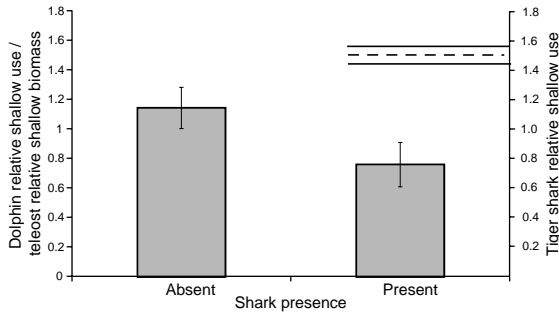
Fig. 3. Influence of tiger shark presence on the distribution of dolphins between shallow and deep habitats (RD_s) relative to the distribution of teleost biomass between habitats (RT_s). A value of 1 indicates a match in the distribution of teleosts and dolphins across habitat patches. Error bars are $\pm$SE. The gray dotted line represents the proportion of tiger sharks in shallow habitats relative to deep ones (RS_s). Solid gray lines are $\pm$SE. If $RS_s = 1$, then there is an equal abundance of sharks in shallow and deep habitats.

The proportion of dolphins found in edge microhabitats relative to shallow interior ones varied significantly with shark presence ($F_{1,22} = 12.9$, P $= 0.002$) but not with zone ($F_{3,22} = 1.5$, P $= 0.25$). When sharks were absent, dolphins were distributed across microhabitats of shallow patches approximately proportional to the distribution of their prey, with 44% of dolphin foraging in edge microhabitats (Fig. 4). When sharks were present, approximately 78% of dolphin foraging was concentrated in edge microhabitats despite lower fish biomass available there than within interior microhabitats. The proportion of dolphins found in deep channels relative to deep open microhabitats did not vary with shark presence ($F_{1,20} = 0.3$, P $= 0.58$) or zone ($F_{3,20} = 0.7$, P $= 0.54$), and was similar to the relative biomass of prey in channels (Fig. 5).
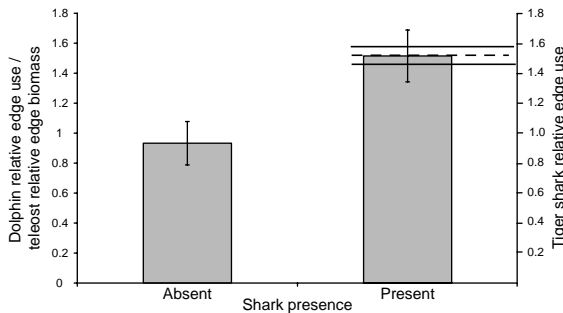

Fig. 4. Influence of tiger shark presence on the distribution of dolphins between edge and interior microhabitats of shallow patches (RD_e) relative to the distribution of teleost biomass between microhabitats (RT_e). A value of 1 indicates a match in the distribution of teleosts and dolphins across microhabitats. Error bars are $\pm$SE. The gray dotted line represents the proportion of tiger sharks in shallow edge microhabitats relative to shallow interior microhabitats (RS_e). Solid gray lines are $\pm$ SE. If $RS_e = 1$, then there is an equal abundance of sharks in shallow interior and shallow edge microhabitats. Note that dolphins shift into edge microhabitats when sharks are present, even though the density of sharks is greater there.
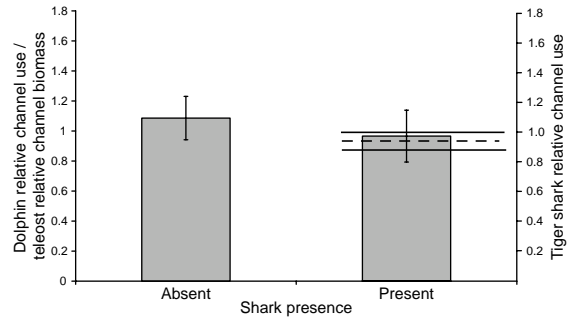

Fig. 5. Influence of tiger shark presence on the distribution of dolphins between channel and open microhabitats of deep patches (RD_c) relative to the distribution of teleost biomass between microhabitats (RT_c). A value of 1 indicates a match in the distribution of teleosts and dolphins across microhabitats. Error bars are $\pm$SE. The gray dotted line represents the proportion of tiger sharks in channel microhabitats relative to open deep microhabitats (RS_c). Solid gray lines are $\pm$SE. If $RS_c = 1$, then there is an equal abundance of sharks in channel and open deep microhabitats.

Discussion

In Shark Bay, dolphins are able to match the distribution of potential prey across multiple spatial scales, including at the scale of 10 s to 100 s of meters. Dolphins were distributed across habitat patches and between micro-habitats of both deep and shallow habitats in proportion to the biomass of prey available in habitat patches or microhabitats when dolphin predators (tiger sharks) were absent. In many marine systems, forager distributions do not coincide with those of their prey at fine spatial scales, which has often been attributed to unpredictability of prey resources at this spatial scale or to anti-predator behavior of prey (Sih 1984, Loggerwell and Hargreaves 1996). In Shark Bay, the biomass of dolphin prey is predictable at multiple spatial scales across seasons and dolphins are able to match the distribution of their prey even at fine spatial scales within the bay.

Dolphins also respond to predation risk at the scale of habitat patches and microhabitats. Foraging dolphins shifted from using habitat patches in proportion to food abundance when sharks were absent, to using the safer, but prey-poor, deep patches disproportionately often when sharks were present (Heithaus and Dill 2002). Within shallow patches, foraging dolphins greatly increased their use of edges when sharks were present despite no differences in the microhabitat distribution of their prey between periods when sharks were present and when they were absent, resulting in dolphin and teleost distributions not coinciding. Within deep habitats, there was no seasonal shift in relative use of the two microhabitats and dolphins showed a foraging preference for channels, where fish biomass was high, over deep open waters. These findings suggest that studies of

forager responses to prey distributions may benefit greatly from understanding spatial and temporal patterns of predation risk and the community context of forager–prey interactions. Indeed, in the dolphin–teleost interaction mismatches between dolphin and fish distributions do not arise from the unpredictability of teleost abundance or anti-predator behavior of teleosts in response to dolphins (mechanisms invoked to explain mismatches in predator and prey abundance in other marine systems; Logerwell and Hargreaves 1996), but instead from dolphin responses to tiger shark predation risk.

It is interesting that, at the scale of habitat patches, dolphins shift away from areas of high shark abundance (shallow patches), but dolphins that do forage in dangerous shallow patches increase their use of edge microhabitats where shark densities are greater than in the interior microhabitats that they largely avoid. While such behavior may seem counterintuitive, it may be explained by examining the subcomponents of predation risk. The risk of predation within a habitat, or microhabitat, can be subdivided into encounter probability and intrinsic habitat risk, where intrinsic risk is determined by attributes of the habitat that influence the probability of death in an encounter situation (Gotceitas and Colgan 1989, Hugie and Dill 1994). At the scale of habitat patches, shallow habitats have greater densities of tiger sharks (higher encounter rates) and are intrinsically more risky, due to limited escape routes and inefficiency of predator detection using echolocation or vision, than deep habitats (Heithaus and Dill 2002). Within these shallow habitats, however, encounter rates and intrinsic risk do not covary across microhabitats. Tiger sharks prefer edge microhabitats over interior ones (Heithaus et al. in press), suggesting higher encounter rates within edge microhabitats. Edges, however, are likely to be intrinsically safer than interior microhabitats. Interior microhabitats are shallower than edge microhabitats, so dolphins are probably more likely to be captured if they encounter a shark within interior microhabitats because there are few directions in which they can escape. Shallower waters also may hinder the ability of dolphins to detect sharks at distances sufficient for escape because echolocation is less efficient due to the scattering of clicks off the surface and bottom (Heithaus and Dill 2002). Finally, in edge habitats dolphins are less vulnerable because they can more easily escape to nearby deep waters where they can more easily out-maneuver sharks (tiger sharks' have limited maneuverability relative to dolphins; Heithaus et al. 2002, Heithaus 2004b). Shifts in the relative use of edge microhabitats by dolphins, with changes in tiger shark abundance argue strongly that intrinsic risk of microhabitats is more important than the encounter rate with sharks in determining microhabitat use. That edge habitats are safer than interior ones is supported by habitat and microhabitat use of dugongs (*Dugong dugon*) and condition dependent behavior of green turtles (*Chelonia mydas*). Turtles in poor body condition are found within interior habitats where seagrass quality is high while turtles in good body condition are found foraging in edge microhabitats with lower seagrass quality (Heithaus et al. unpubl.). In addition, dugongs reduce their use of habitat patches with a low proportion of edge microhabitat and begin using edge microhabitats to a greater extent as tiger shark predation risk increases (Wirsing et al. 2005).

Our finding that intrinsic habitat risk is important to dolphin microhabitat use decisions is consistent with theoretical predictions. Game theoretical models of foragers and their predators, in this case dolphins and tiger sharks, predict that they should achieve stable distributions, when prey select habitats on the basis of intrinsic risk rather than predator or food densities (Hugie and Dill 1994, Heithaus 2001a). At the patch scale, both intrinsic habitat risk and encounter rates with tiger sharks are greater in shallow habitats (Heithaus and Dill 2002) making it impossible to determine their relative influences at the scale of patches.

The relative abundance of tiger sharks, dolphins, and teleosts across habitats and microhabitats reveals that spatial variation in predator encounter rates and intrinsic risk influences the likelihood of predator and prey distributions being linked at multiple spatial scales in a three-tier predator prey interaction (Fig. 6). At the scale of habitat patches and within microhabitats of both deep and shallow habitats, dolphins match the distribution of teleost prey when tiger sharks are absent, which is consistent with the predictions of an ideal free distribution (Fretwell and Lucas 1970). Such a linkage of distributions probably is achieved because aquatic vegetation provides a refuge from multiple predators (Gotceitas and Colgan 1989), and teleosts cannot improve their chances of escape in an encounter situation by shifting habitats or microhabitats. Therefore, teleost distributions are effectively fixed by the presence of refuges from non-dolphin predators, thereby allowing dolphins to match the distribution of their prey resources.

When tiger sharks are present, neither tiger shark and dolphin nor dolphin and teleost distributions coincide at the scale of habitat patches. However, the distribution of dolphins is similar to that of teleosts across deep microhabitats, with both being more abundant in channels, while sharks are slightly more common in open microhabitats (Heithaus et al. in press) and thus are not distributed relative to dolphins. Sharks are unlikely to respond to dolphin distributions, which are infrequent prey (Simpfendorfer et al. 2001, Heithaus 2001d), but rather to the distribution of other, more common, prey. Because of the microhabitat differences
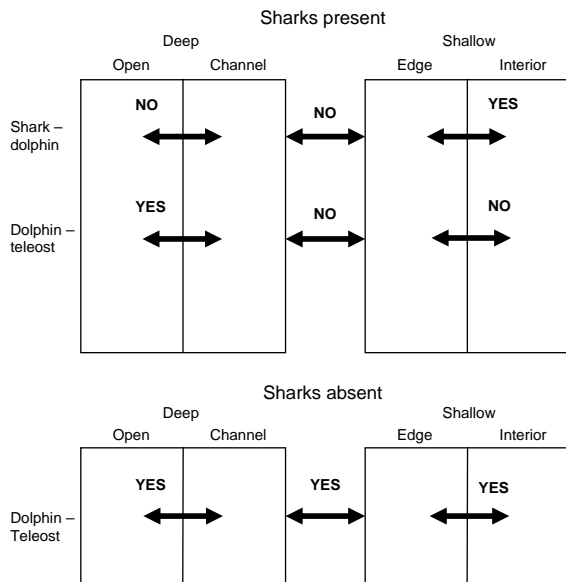
Fig. 6. Schematic drawing of the effect of spatial scale on the distributions of dolphins relative to their predators and prey. Dolphins are distributed within and between habitats proportionate to teleost abundance when tiger sharks are largely absent. When shark density is high, dolphin and teleosts distributions are only similar across deep microhabitats.

in intrinsic risk within shallow microhabitats, dolphins are found in greater densities in the preferred microhabitat of tiger sharks and are not distributed within shallow areas according to teleost density. While intrinsic risk is likely to be responsible for much of this pattern, tiger sharks are still abundant in interior microhabitats, where prey are more easily captured, but probably prefer edge microhabitats because of the relatively high density of alternative, and more common, prey types including dugongs and sea turtles (Heithaus et al. in press, Wirsing 2005). Indeed, theory predicts that the presence of alternative prey may have a large impact on the distribution of top predators as well as on prey species that share a common predator (Heithaus 2001a). Thus, studies of habitat and microhabitat use will benefit greatly from considering the community context of interactions and spatial variation in both predator abundances and intrinsic habitat risk.

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