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Towards a Standardized Approach of Cetacean Habitat: Past Achievements and Future Directions

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Abstract

The understanding of what habitat means for an organism as well as the underlying factors driving patterns of habitat use is still unknown for many species. Cetacean habitat has been described using a range of methodologies and variables measured over various temporal and spatial scales that are often author-dependent. However, in order to develop an objective and sound understanding of what habitat actually means for cetaceans, a standardized approach needs to be developed. Here, after briefly reviewing the fundamental differences between terrestrial and marine habitats, we highlight the difficulty in defining a marine habitat, with a special focus on marine mammals. We subsequently provide six recommendations by which future cetacean habitat studies might be approached. This recommended approach aims to amend the way in which we think about and undertake investigations into cetacean habitat. It is believed that through this broadened approach, future cetacean habitat studies will increase our understanding of underlying driving factors of cetacean habitat, rather than just describing distribution patterns. Finally, it is stressed how the proposed approach will be more directly applicable within management frameworks and of benefit to conservation initiatives.

Keywords

Cetacean, Dolphins, Whales, Habitat, Modelling, Management, Conservation

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1. Introduction

The study of habitat is essential for understanding the biological and ecological requirements of animals as well as the strategies they employ to fulfill their needs [1]. In addition, habitat information is a fundamental prerequisite for the implementation of both management and conservation strategies [2]. However, the definition of habitat is still a contentious one, and its use is far from being consistent [3]. In particular, there is a general lack of unified definition in both terrestrial and marine ecological studies (**Table 1** and **Table 2**). As a further example, a review of the use of the term in terrestrial studies found that 82% of articles reviewed, used habitat terminology imprecisely [4].

Table 1. Non-exhaustive review of habitat definitions applied and/or discussed in the terrestrial ecology literature.

Definition	Reference
A species or population unit; an abstraction of the essential physical factors and theco-habitant biota, in a locality where individuals of that population regularly live and reproduce	[82]
Place/space where an organism lives	[83]
The area of land, water and airspace required for the normal needs and survival of a species	[84]
Area in which a wildlife community exists	[85]
Location in which organisms live, or characterized by predominant plant or animal life	[13]
Resources and conditions present in an area that produce occupancy—including survival and reproduction—by a given organism	[4]
Where an animal lives that can be characterized by dominant plant forms or physical features	[86]
The resources an conditions present in an area that produce occupancy, including survival and reproduction, by a given organism	[3]
Place where an animal lives, or, the collection of resources and conditions necessary for its occupancy, or, a set of specific environmental features that, is equated to a plant community, vegetative association or cover type	[87]
A place where an animal resides	[88]
The abiotic components of the environment only	[11]
The physical and chemical components of an organism's environment, including the biotic environment to emphasize that an organism must integrate and adapt to all the elements of its surroundings including those that are living and those that are not	[89]
Description of the physical space, at a particular scale of space and time, where an organism actually or potentially lives	[10]

Table 2. Non-exhaustive review of habitat definitions applied to general or specific groups of marine organisms.

Definition	Species/order/taxa	Reference
A place in which a fish, a population or assemblage can find the physical or chemical features required for life, e.g. suitable water quality, migration routes, spawning grounds, feeding sites, resting sites, and shelter from predators and adverse weather	Fish	[90]
Areas vital to the survival of a marine species at some phase in its life cycle	Various species	[91]
The functioning ecological units required for successful breeding and foraging	Mammals	[92]
The place where an organism can be found	Various species	[93]
Each species lives within a certain environment, whereby it has a preference for a combination of environmental factors, e.g. substratum, temperature, salinity and hydrodynamic conditions that it is able to live within	Various species	[94]
Parts of a cetacean's range, either a species or population of that species, essential for the day-to-day survival, as for maintaining a healthy population growth rate. Areas used for feeding, breeding, raising calves, migrating	Cetaceans	[7]
Features related to basic needs e.g. prey; refuge from predators; suitable conditions for reproduction including mating and rearing young, resting, and moulting; and safety from extreme environmental events	Mammals	[89]

Definition and research into habitat have frequently been identified as crucial for cetacean management and conservation (e.g. [2] [5]-[8]). However, a consistent definition and understanding of what habitat actually means for cetaceans is still lacking. As a consequence, there is limited information and understanding of habitat characteristics for most species [9]. In order to advance our understanding of the underlying drivers and processes that influence cetacean habitat, studies need to develop more a standardized and objective approach in which to examine them. This broadened approach will ultimately assist in the development and implementation of effective management, conservation and threat mitigation strategies.

In this context, the aims of the present work are: 1) to provide what we believe are representative examples between terrestrial and marine environments; 2) to highlight the specific features of marine environments that may contribute to the current lack of consensus in defining cetacean habitat, 3) provide a non-exhaustive review of how cetacean habitat has previously been studied, including modeling approaches and 4) to provide objective recommendations on how to develop an approach to studying habitat in order to advance cetacean ecology, and ultimately conservation and management efforts.

2. Terrestrial versus Marine Habitats

Typically, habitat in its simplest terms is defined as the physical environment, where an organism actually or potentially lives [10]. In addition, it has also been expanded to include the resources and environmental features present in an area which influences occupancy [4]. Habitat can also be thought of as a concept, used to link potential relationships between an organism and its physical and chemical environment [11]. However, a mechanistic understanding of this concept and how particular features influence organisms is still critically lacking [10].

Accurately describing and understanding the processes that determine the distribution of organisms is often constrained by the environment itself. Terrestrial and marine ecosystems are both spatially heterogeneous, comprised of ecological entities such as forests, hills, deserts, sea grass beds, seamounts and coral reefs, but also vary in time from diel to annual cycles (e.g. [12]). In terrestrial ecosystems, habitat is often defined by the presence of relatively persistent vegetation and animal life [13]. For example, the boundaries between the biotic and abiotic properties characterizing structurally diverse terrestrial environments (**Figure 1**) are easily observed and identifiable (e.g. vegetation patches, sedimentary rocky areas, gorges and slopes of cobbles and boulders). In many cases, the relatively immediate accessibility and visibility of the terrestrial environment, enhances our capacity to identify and observe environmental differences.

Figure 1. A terrestrial landscape, the Kata Tjuta (Northern Territory, Australia), illustrating how the boundaries between the biotic and abiotic features of a structurally diverse two-dimensional terrestrial habitat are easily identifiable and quantifiable, e.g. vegetation patches, sedimentary rocky areas, gorges and slopes of cobbles and boulders. Image credit: L. Seuront.

In contrast, most marine environments are characterized by a limited number of landmarks both above and beneath the surface (**Figure 2**). Marine organisms typically live in a fluctuating and heterogeneous three-dimensional water mass. In addition, the inaccessibility of most of the World's ocean, and the logistical considerations inherent in effectively studying marine organisms once underwater, places additional limitations on how to define habitat for an organism, a species or a community. The characteristic wide-ranging and migratory nature of many marine animals, including cetaceans, often means that habitat boundaries are difficult to define ([7]; **Figure 2**), and may change on a temporal basis. Furthermore, regions within the World's Oceans are often defined by broad, general definitions such as open ocean or coastal waters, although specific sea surface temperature signatures such as warm and cold core eddies (**Figure 3(A)**) and thermal frontal zones (**Figure 3(B)**) can be specified. These broad classifications are frequently applied to species such as cetaceans, particularly those rarely sighted or cryptic species [14]. While these areas may be relatively distinct (**Figure 3(C)**), general classifications still lack a definitive understanding of what habitat actually means. As a consequence, the definition of marine habitat often seems arbitrary and in most cases non-existent. The application of the term habitat is often inconsistent even between marine animals of the same species or taxa (**Table 2**). These definitions highlight those potential factors (e.g. environmental factors) considered to be essential for the animals but again lack a thorough consideration of how the animal actually interacts with and relies on its environment.

In addition, habitat for many organisms (e.g. migratory birds, cryptic species), is often characterized using a limited number of observations recorded at specific encounter locations. Cetaceans are no exception, with habitat often described using only sightings or environmental measurements recorded at the surface, when the animals are exposed [15]-[19]. This strategy, however, disregards the properties and characteristics of the habitat concealed underneath, vertical structure of the water column. In contrast to terrestrial systems where environmental features are readily accessible and visible (**Figure 1**), in the marine environment it is considered much more difficult to gather relevant habitat information at depth. This again, potentially highlights the inaccessibility and the logistics of conducting research within these areas. Whilst some techniques (e.g. remote sensing imagery, animal borne sensors) can offer new perspectives and insight into detailed understanding of the vertical structure of the water column, they do not directly address the issue of habitat in order to provide sufficient information. Hence, in the marine environment, little information about the relations between species and their specific environments exists, despite their significance [20].

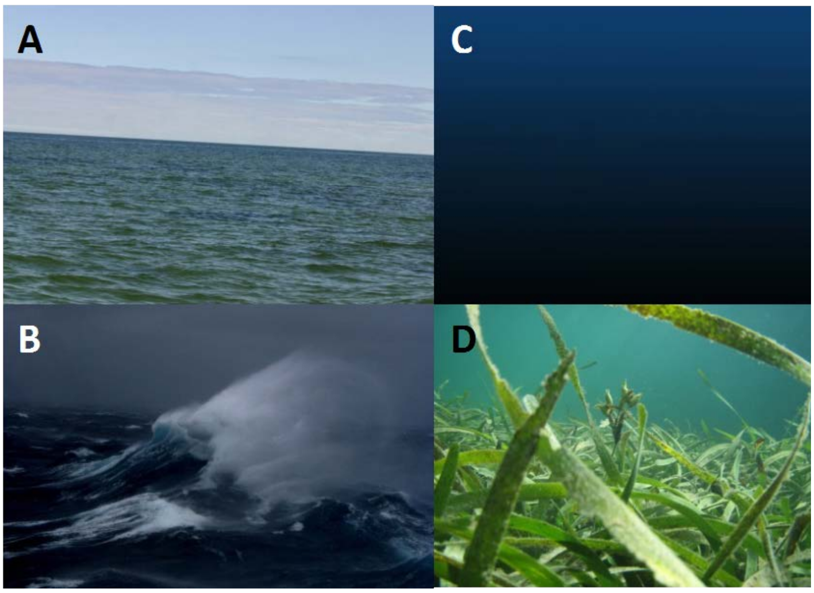


Figure 2. Marine landscapes, seen from above the surface in Gulf St. Vincent, South Australia (A) in stormy weather in the Southern Ocean ((B); 53˚S, 145˚E), and beneath the surface in open water (C) above a seagrass bed in Louth Bay, South Australia (D), illustrating the difficulties in identifying landmarks and both abiotic and biotic properties leading to define cetacean habitat. Image credits: N. Cribb (A); V. Van Dongen-Vogels (B); L. Seuront ((C), (D)).

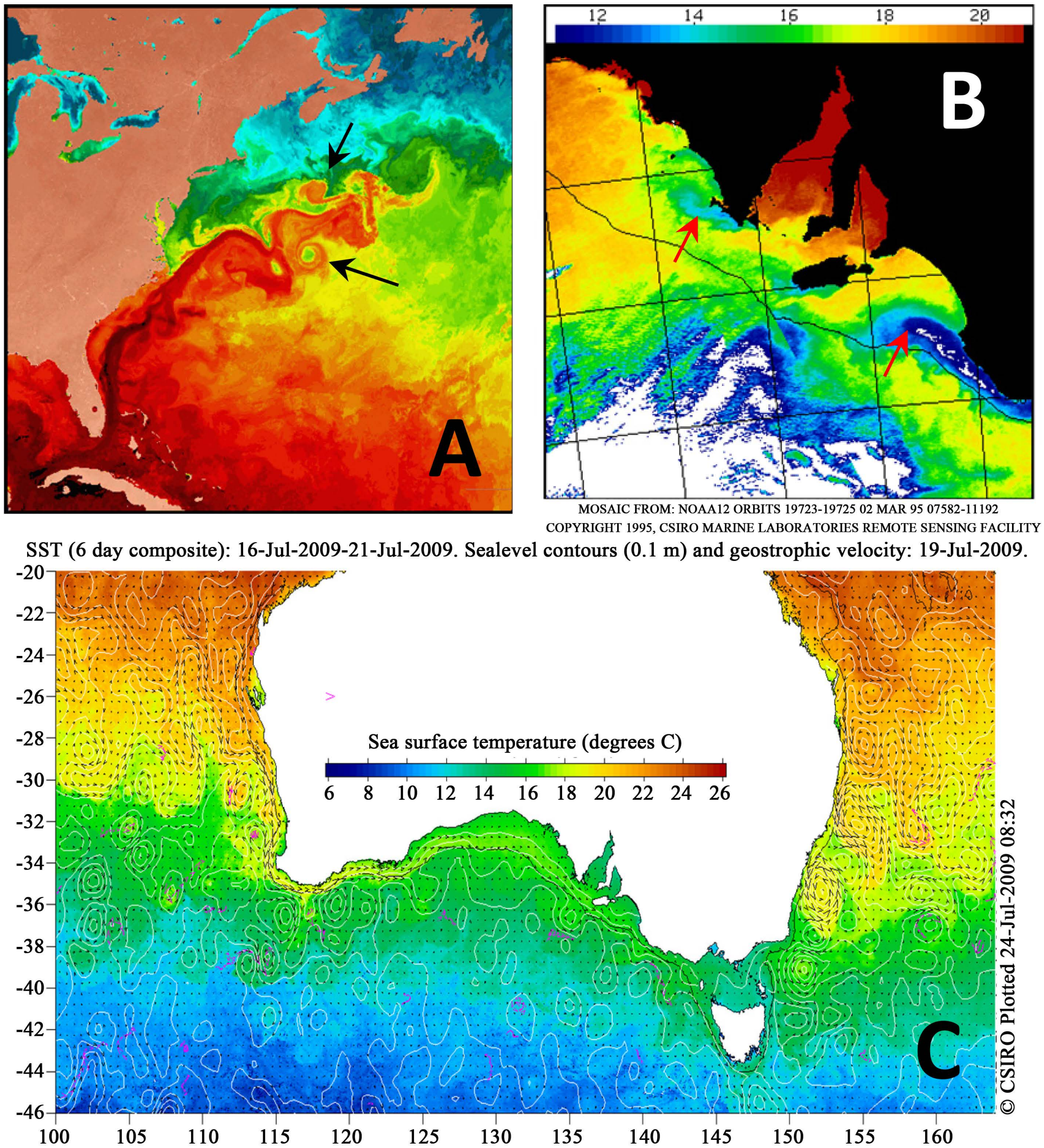


Figure 3. Illustration of typical sea surface temperature signatures of (A) the meandering Gulf Stream showing basin-scale thermal fronts and related warm and cold core eddies (black arrows); (B) upwelling events on South Australian shelf waters (red arrows), and (C) the Australian subtropical front that may be used to identify provinces inhabited by various cetacean species. Image credit: Ocean Remote Sensing Group, Johns Hopkins University Applied Physics Laboratory (A), and CSIRO ((B); (C)).

3. The Concept of Cetacean Habitat So Far

Cetacean species exhibit a wide range of distribution patterns across all parts of the World's Oceans [5] [21]-[26] As individuals and populations range widely and are not easy to observe directly, the concept of habitat is therefore difficult to grasp and define [27]. The wide diversity of cetacean species in general, makes our ability to understand their habitat more problematic. For example, many delphinids are widely distributed, with smaller populations inhabiting various locations and climatic regions, whilst in contrast larger mysticetes follow migrational routes each year to familiar calving areas [28]. The intrinsic difference in distributions across temperate and tropical, and coastal and offshore waters between the cetacean species, not only demonstrates their great ecological flexibility [29], but also ultimately links them to their habitat. In addition, the distinction between life history strategies and the biological requirements of the different species potentially influences their choice, and utilization of specific habitats in the marine environment; something which is also commonly dismissed in many habitat studies.

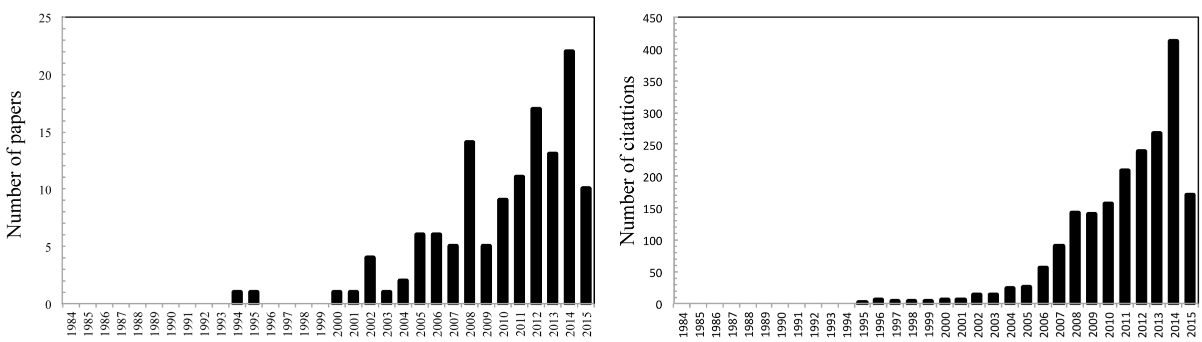
Critical cetacean habitat in a broad sense has previously been defined as "those parts of a cetacean's range either a species or population that are essential for the day-to-day survival and maintenance of a steady population growth rate, including those areas essential for specific behaviors such as mating, feeding and migrational routes" [7]. Cetacean habitat, and more specifically delphinid habitat, has typically been defined by investigating a number of abiotic and biotic factors ranging over various spatial and temporal scales thought to drive their distribution [30]-[36]. Factors previously investigated range from the physical and chemical features of the environment, such as water temperature, depth, salinity, topography and distance from shore, benthic habitat characteristics, and the presence of vessels, and preys and predators (**Table 3**). Measurement of these habitat variables was typically obtained using a wide variety of methodologies (e.g. *in situ* measurements, remotely sensed, obtained by boat or land based techniques), levels of precision (*in situ* vs. remotely sensed) and scales (temporal, spatial). Furthermore, variables used to assess habitat (even for a given species) were typically author and study dependent. For instance, a non-exhaustive review of pertinent studies of bottlenose dolphins (*Tursiops* sp.) clearly demonstrates the variety of both habitat measurements and spatio-temporal scales used [17] [37]-[40].

Among the variables used to assess cetacean habitat, sea surface temperature represents a common measurement that is often measured with a variety of scales and resolutions (**Figure 3**). For instance, [17] compared the distribution of white-sided (*Lagenorhynchus acutus*) and common (Delphinus delphis) dolphins off the coast of New Zealand with sea surface temperature and salinity measured from the survey vessel at the time of a dolphin sighting. In comparison, water temperature measurements accessed from remote sensing data was used to investigate seasonal distribution changes in striped dolphins (*Stenella coeruleoalba*) in the Ligurian Sea [41]. Of further note is the typically small number of environmental variables measured in many studies despite the high plausibility of other factors being instructive in describing habitat [42]-[44]. This consideration and narrowed selection of assessed variables should therefore caution our application of some habitat studies for progressing management objectives and conservation strategies. More specifically, a thorough understanding of constraints, methodology and objectives needs to be made to ensure that the results of habitat studies are not being confounded by the concentration of the researcher's effort and measurement tools or access [45].

4. On the Contribution of Habitat Modeling to Cetacean Ecology

Statistical habitat modeling, although still a relatively recent topic of research, is increasingly being applied to help answer questions regarding the ecology of many cetacean species [46]. Since the first paper there has been a significant growth and increase in this topic (**Figure 4**), which suggests a field in rapid development.

Typically, the aim of statistical habitat modeling is to help predict and explain variation in the distribution and density of cetaceans, as well as to predict key locations by correlating observations of animals with various environmental variables [47] [48]. However, these efforts may describe correlations between variables, but they generally lack the ability to elucidate our ecological understanding of the relationships between cetaceans and their marine environment.



(A) (B)

Figure 4. Number of papers containing the words cetacean, habitat and model in their topics published per year over the last 20 years (A) and their subsequent number of citations per year (B).

Table 3. Common name, location and examples of variables used to define habitat and distribution in global delphinid studies from 1968 to present.

Common name	Location	Variables used to define habitat	Reference
Common dolphin, Dusky dolphin, Hourglass dolphin	South Pacific	SST[a]	[15]
Common bottlenose dolphin	Gulf of Mexico	Distribution patterns related to tidal occurrence, time of day, season	[95]
White-sided dolphin, Common dolphin	North Atlantic	SST, salinity, bottom topography	[95]
Common bottlenose dolphin	Moreton Bay	Distance from shore	[96]
Common bottlenose dolphin	Gulf of California	Behavioral and range patterns related to estuarine vs. non-estuarine habitat types, depth, Secchi depth	[97]
Pilot whale	North Atlantic	Depth, bottom topography, SST	[29]
Risso's dolphin	Gulf of Mexico	Depth, depth gradient	[42]
Common bottlenose dolphin	Moray Firth	Movement patterns and seasonal distribution determined through photo-identification	[16]
Indo-Pacific humpback dolphin	Algoa Bay	Distance to shore, depth, behavioral activities related to physical habitat features	[98]
Tursiops sp.	Shark Bay	Reproductive success, depth, SST	[99]
Common bottlenose dolphin	Gulf of Mexico	Foraging behavior, prey presence related to benthic habitat characteristics	[100]
Hector's dolphin	Porpoise Bay	Photo-identification & land based theodolite fixes to determine spatial, temporal distribution patterns	[101]
Indo-Pacific bottlenose dolphin	Shark Bay	Effect of prey abundance, shark presence on habitat use & group size	[31]
Tursiops sp.	Shannon estuary	Encounter locations related to benthic topography, depth, benthic slope	[38]
Common bottlenose dolphin	Moray Firth	Spatial, temporal distribution related to tidal cycle, tidal front	[102]
Common bottlenose dolphin, Atlantic spotted dolphin	Gulf of Mexico	Depth, SST, salinity, Chl. *a*[b]	[103]
Common bottlenose dolphin	Moray Firth	Foraging observations related to local submarine habitat characteristics	[32]
Common bottlenose dolphin	Chesapeake Bay	SST and Chl. *a* used as surrogates to monitor dolphin and prey movements	[104]
Common bottlenose dolphin	Mid-Atlantic Bight	SST, Chl. *a*	[105]
Atlantic spotted dolphin, Pantropical spotted dolphin, Clymene dolphin, Spinner dolphin, Striped dolphin	South West Atlantic	Depth, SST	[106]
Snubfin dolphin, Indo-Pacific humpback dolphin	Cleveland Bay	SST, proximity to environmental features, bathymetry	[107]
Peale's dolphin	Straight of Magellan	Dolphin presence and behavioral activities related to kelp beds	[108]
Tursiops sp.	Shark Bay	Aquaculture presence	[33]
Tursiops sp.	Shark Bay	Vessel effect on abundance	[34]
Spinner dolphin	Central Tropical Pacific	Surface turbidity, current, swell height, distance to shore, vessel presence	[34]
Snubfin dolphin, Indo-Pacific humpback dolphin	Cleveland Bay	Depth, distance to physical environmental features	[109]
Common dolphin, Striped dolphin, Common bottlenose dolphin, Harbour porpoise, Pilot whale	English Channel	Distribution, encounter rate, bathymetric preference	[19]

Continued

Striped dolphin	Ligurian Sea	Chl. *a*, SST	[41]
Common dolphin	Mediterranean Sea	Calf presence, inter-specific relationships, behavior, Chl. *a*, SST, depth, slope of seabed	[110]
Indo-Pacific bottlenose dolphin	Gulf St Vincent	Depth, SST, salinity, dissolved oxygen, turbidity, distribution in relation to benthic characteristics	[39]
Harbour porpoise	English Channel	Sightings related to diurnal and tidal patterns	[111]
Common bottlenose dolphin	Barataria and Caminada Bays	SST, salinity, dissolved oxygen, depth, turbidity, distance to shore	[40]
Spinner dolphin	Red Sea	SST, distribution related to swimmer presence	[57]
Common dolphin	Gulf St Vincent	Depth, SST, latitude, longitude	[112]

[a]SST: Sea Surface Temperature; [b]Chl. *a*: chlorophyll *a* concentration.

From a non-exhaustive review, we show as aforementioned for field-based habitat studies that modeling habitat studies do not converge in their approaches, methodologies, spatial and temporal scales and analyses even when they target the same species (**Table 4**). Some studies are vague in their definition of a potential focus species as well as an ecological question, and often the focus species is then defined afterwards depending upon what species were observed during surveys. The overall objective of many studies is then often limited to predict where and when cetaceans are present (e.g. [49]). However, some studies do attempt to explain this presence further by linking them to features of the physical and biological oceanographic properties of their environment [48]; these properties have either been assessed using remote sensing data (e.g. sea surface temperature, sea surface height), variables measured *in situ* (e.g. depth, mixing layer thickness) or even modeled environmental data such as prey densities [50], hence allow to cover a very wide range of spatial and temporal scales; see **Table 4** for further examples. There is, however, a strong study-to-study variability in the abiotic properties considered even in modeling studies dealing with similar environments and species (**Table 4**). Biotic variables are also dramatically under-represented (especially when compared to physical variables) in most of the studies reported here (**Table 4**). Similarly, biotic factors that may be critical to understand cetacean habitat use such as behavioral and life history strategies, have still been seldom used in habitat modeling studies ([48]; **Table 4**). Besides, studies that incorporate field-based visual and acoustic surveys [51]-[53] often lack information about the physical and vertical properties of the environments (**Table 4**). Also note that most synoptic studies that used remote sensing data, critically lack information about the vertical structure of the water column [54]. The aforementioned limitations of habitat modeling studies—which are by no means a criticism of their results and do not detract from the central point of their work—hence suggest that although habitat modeling studies provide valuable information on where and when cetaceans may be over space and time, they still ultimately lack the power in which to truly understand the mechanistic links between the presence and behavior of cetaceans and the nature of their environment.

As a conclusion, statistical habitat modeling is undeniably a useful and promising tool to predict cetacean distributions as a function of range of descriptors (**Table 4**), in particular for those large whale and offshore cryptic species which lack baseline data and are often difficult to access. However, this approach still does not converge in the approach followed (**Table 4**), hence may prevent future progress in our ability to provide further insight into animal ecology. As stressed in the present work and in the recommendation below, there is a genuine need to refine modeling methods to move beyond correlations towards a mechanistic understanding of the processes that interact to create cetacean habitat and try to provide a more ecological explanation for their presence. Ultimately, this may also help to bridge the gap between fundamental research and conservation and management initiatives.

5. How to Fill in the Gaps?

To increase our understanding of cetacean habitat, we suggest to develop a more systematic and objective approach to cetacean habitat research. In particular, we stress the need to identify the underlying influences driving habitat, for example physical and chemical environmental features, social and behavioral factors, predation and anthropogenic pressures in order to determine how cetaceans interact with and use their environment. With this

Table 4. Location, species and environmental variables used in habitat modeling studies to define cetaceans and habitat distributions.

Location	Species	Environmental variables used to model habitat: Abiotic	Environmental variables used to model habitat: Biotic	Reference
Nova Scotia	M_3, M_4, M_7, M_8, O_1, O_5, O_8, O_{15}, O_{19}, O_{24}, O_{25}	Depth, slope, $SST_{in\ situ}$[a]		[113]
California	O_{25}, O_{31}	$SST_{in\ situ}$, salinity, depth		[114]
British Columbia	M_3, M_4, M_5, M_8, O_1	Depth, slope, $SST_{in\ situ}$, salinity,	Historical whaling data	[115]
Mid-west North Atlantic Ocean	M_4, M_7, M_8, O_1, O_4, O_8, O_9, O_{15}, O_{18}, O_{19}, O_{20}, O_{21}, O_{25}, O_{32}, *Mesoplodon* spp.	$SST_{in\ situ}$, front occurrence, depth, slope		[116]
Spain	O_1, O_4, O_5, O_8, O_{18}, O_{19}, O_{24}, O_{25}	Depth, slope, SST_{sat}		[117]
Faroe-Shetland Channel	Oceanic dolphins	$SST_{in\ situ}$, salinity, depth, slope, ambient noise	Chl.$a_{in\ situ}$[b]	[118]
Eastern Tropical Pacific	O_4, *Mesoplodon* spp.	Thermocline depth and strength, $SST_{in\ situ}$, salinity, depth, slope	Chl.$a_{in\ situ}$	[50]
Eastern Tropical Pacific	O_7, O_8, O_9, O_{10}, O_{11}, O_{12}, O_{13}, O_{14}, O_{18}, O_{19}, O_{20}, O_{22}, O_{23}, O_{24}, O_{25}, O_{26}, O_{27}, O_{28}	$SST_{in\ situ}$, salinity, thermocline depth and strength, depth, slope	Chl.$a_{in\ situ}$	[119]
Western Antarctic Peninsula	M_8, M_6	Acoustic volume backscatter, depth, slope, $temperature_{in\ situ}$	Chl.$a_{in\ situ}$	[120]
South central Alaska	O_2	Depth, flow accumulation		[121]
Hawaiian Archipelago	M_8	Depth, SST_{sat}		[51]
Northern Adriatic Seas	O_{19}	O_2 saturation, $temperature_{in\ situ}$, density anomaly, turbidity, depth , salinity, pH, turbidity	IVF[c]	[8]
Bay of Biscay	O_{19}, O_{24}, O_{25}	Distance		[122]
SW Mediterranean Sea	O_{25}	Depth, slope, SST_{sat}, scattering layers	Chl. a_{sat}, presence of calves, interspecific relationships, behavior	[110]
Strait of Gibraltar	O_1, O_7, O_8, O_{19}, O_{24}, O_{25}	Depth, slope		[123]
Central Mediterranean Sea	O_{18}, O_{19}, O_{24}	Depth, slope, SST_{sat}	Chl.a_{sat}	[124]
Pelagos sanctuary (Mediterranean Sea)	M_4, O_{24}	Depth, slope, SST_{sat}	Chl.a_{sat}	[125]
North-western Mediterranean	O_1, O_9, O_{18}	Depth, slope, SST_{sat}, fronts, salinity	Chl.a_{sat}	[52]
Eastern tropical pacific	O_{24}, O_{23}, O_{25}, O_{18}	$SST_{in\ situ}$, salinity, thermocline depth and strength, depth, temperature fronts	Chl.$a_{in\ situ}$	[126]
Mid Atlantic Ridge	M_5, O_1	Bathymetry, slope, flow velocity, water level gradient, temperature and salinity gradients		[127]
Florida Bay, USA	O_{19}	$Temperature_{in\ situ}$, salinity, turbidity, dissolved O_2, benthic type	Chl.$a_{in\ situ}$ Dolphin prey per unit effort	[128]
Scotland	O_{19}, O_{32}	Depth, slope, distance, $SST_{in\ situ}$, sediment type, salinity		[129]
Greater Minch, Scotland	O_{32}	Depth, bathymetry, distance, tidal conditions		[130]
Gulf of Maine	M_1		Modeled prey densities, arrival date of whales in study location, sightings per unit effort	[50]

Continued

Sundarbans mangrove forest, Bangladesh	O_6, O_{33}	Salinity, depth, turbidity, temperature$_{in\ situ}$, channel width, convergences		[131]
California current	M_3, M_4, M_8, O_1, O_{14}, O_{18}, O_{24}, O_{25}, O_{28}, O_{31}	SST$_{in\ situ,\ sat}$, frontal regions, oceanic zone, depth, slope		[132]
Western Mediterranean	O_{24}	Absolute dynamic topography, SST$_{sat,\ in\ situ}$, absolute geostrophic velocity, sea level anomaly, geostrophic velocity anomaly, depth		[133]
Inner Hebrides, Scotland	O_{32}	Tidal conditions, depth, slope, sediment type		[134]
Argentina	O_{15}	Depth, slope, SST$_{sat}$		[135]
Chile	M_3, M_7, M_8, O_4, O_7, O_{10}, O_{17}, O_{19}, O_{30} unidentified mysticetes and unidentified odontocetes	Depth, channel width, coastline complexity		[136]
Oman	M_8, *Balaenoptera* spp.	Slope, depth		[137]
Patagonia, Argentina	O_{15}, O_{29}	Depth, SST$_{sat}$	Chl. a_{sat}	[138]
Balearic Islands	O_1	Depth, slope, SST$_{sat}$, SS height deviation, surface wind direction	Chl. a_{sat}	[139]
Southern Californian Bight	O_{14}, O_{18}	Echolocation click occurrence, lunar duration, upwelling index, SST$_{sat}$, interaction of week and region	Chl. a_{sat}	[53]
Southern ocean	M_7	Depth, sea ice cover, distance, distance, slope	Chl. a_{sat}	[140]
Hebrides, Scotland	M_6	Bathymetry, slope, SST$_{sat}$, tidal current, depth	Chl. a_{sat}, sandeel occurrence	[141]
Pelagos sanctuary (Mediterranean Sea)	M_4, O_1, O_4, O_8, O_{18}, O_{19}, O_{24}	Depth, slope		[142]
California current	M_4, O_{24}, O_{31}	Depth, slope, SST$_{sat}$		[143]
Atlantic east coast and Gulf of Mexico	M_1, M_8, O_1, O_7, O_{19}, O_{20}, O_{21}, O_{22}, O_{24}, O_{25}, O_{32}, Baleen whale spp., Beaked whale spp., *Kogia* spp., *Lagenorhyncus* spp., Pilot whale spp.,	Depth, distance to shore, monthly SST distance to continental shelf break		[144]
British Columbia	M_8	Depth, slope, SST$_{sat}$	Chl. a_{sat}	[145]
St Lawrence River estuary, Canada	M_3	Depth, slope, feeding	Behavior	[146]
California current, Eastern Tropical Pacific	M_3, M_4, M_8, O_1, O_3, O_4, O_{14}, O_{18}, O_{24}, O_{25}, O_{28}, O_{31}, *Mesoplodon* spp.	Depth, slope, SST$_{sat}$, salinity, mixed layer depth	Chl. $a_{in\ situ}$	[147]
Hawaiian Islands	O_{22}	Aspect variety, bay area, coastline to area of a bay ratio, depth, distance, proportion of bay area with depths < 250 m		[148]
Scotland, west coast	O_{32}	Depth, slope, current speed, tidal conditions, sediment type		[149]
Scotland	O_{18}	Depth, slope, sediment type	Prey distribution	[150]
Australasia	M_2	Depth, slope, temperature$_{sat}$, mixed layer depth, currents	Historical whaling data, Chl. a_{sat}	[151]

[a]Sea surface temperature referred to as SST$_{sat}$ hereafter from satellite data, and as SST$_{in\ situ}$ when measured *in situ*. [b]Chlorophyll *a* concentration referred to as chla$_{sat}$ from satellite data, as chla$_{in\ situ}$ when measured *in situ*. [c]IVF *in vivo* fluorescence measured *in situ* as a proxy of chlorophyll *a* concentration. The letters M and O respectively stands for Mysticetes and Odontocetes; M_1: *Eubalaena glacialis*, M_2: *Eubalaena australis*, M_3: *Balaenoptera musculus*, M_4: *Balaenoptera physalus*, M_5: *Balaenoptera borealis*, M_6: *Balaenoptera acutorostrata*, M_7: *Balaenoptera bonaerensis* and M_8: *Megaptera novaeangliae*. O_1: *Physeter macrocephalus*, O_2: *Delphinapterus leucas*, O_3: *Berardius bairdii*, O_4: *Ziphius cavirostris*, O_5: *Hyperoodon ampullatus*, O_6: *Orcaella brevirostris*, O_7: *Orcinus orca*, O_8: *Globicephala melas*, O_9: *Globicephala macrorhynchus*, O_{10}: *Pseudorca crassidens*, O_{11}: *Feresa atenuata*, O_{12}: *Peponocephala electra*, O_{13}: *Steno bredanensis*, O_{14}: *Lagenorhynchus obliquidens*, O_{15}: *Lagenorhynchus obscurus*, O_{16}: *Lagenorhynchus acutus*, O_{17}: *Lagenorhynchus australis*, O_{18}: *Grampus griseus*, O_{19}: *Tursiopus truncatus*, O_{20}: *Stenella attenuate*, O_{21}: *Stenella frontalis*, O_{22}: *Stenella longirostris*, O_{23}: *Stenella longirostris orientalis*, O_{24}: *Stenella coeruleoalba*, O_{25}: *Delphinus delphis*, O_{26}: *Delphinus capensis*, O_{27}: *Lagenodelphis hosei*, O_{28}: *Lissodelphis borealis*, O_{29}: *Celphalorhyncus comersonnii*, O_{30}: *Celphalorhyncus eutropia*, O_{31}: *Phocoenoides dalli*, O_{32}: *Phocoena phocoena* and O_{33}: *Platanista gangetica*.

in mind, a number of factors should be considered on how to approach and develop methodologies in which to investigate cetacean habitat. The following six recommendations—synthesized as a logical flow chart in **Figure 5**—demonstrates how future studies could become more targeted and effective in defining and describing habitat. The purpose of this outline is to progress towards a more standardized and objective approach to habitat studies. Specifically, the six recommendations developed hereafter are illustrated using selected case studies from the primary literature on both well-documented and more cryptic species to demonstrate the generality of the proposed approach.

5.1. Identify the Rationale for Studying Habitat

In order to describe habitat for a species or a population, the end objectives behind conducting the study firstly need to be clearly identified and addressed. Habitat characteristics should be considered on a case-by-case basis, as each species, population and location will inherently require different strategies, requirements and management considerations. An initial consideration should be the identification of research objectives, which may include 1) assisting in the development and implementation of conservation and management strategies (e.g. marine parks and reserves); 2) developing ecosystem based models; and 3) increasing the biological understanding of the animal's biology and ecology, or for mitigation purposes. For example, the habitat characteristics of the Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) were specifically investigated with the intention to provide baseline information for a newly declared dolphin sanctuary in Adelaide, South Australia [39]. Little information existed about habitat characteristics of bottlenose dolphins in this area; hence specific habitat information was required in which to assist developing management efforts. The variety of environmental types within the declared sanctuary boundaries where dolphins were regularly sighted, were taken into consideration (e.g. ben-

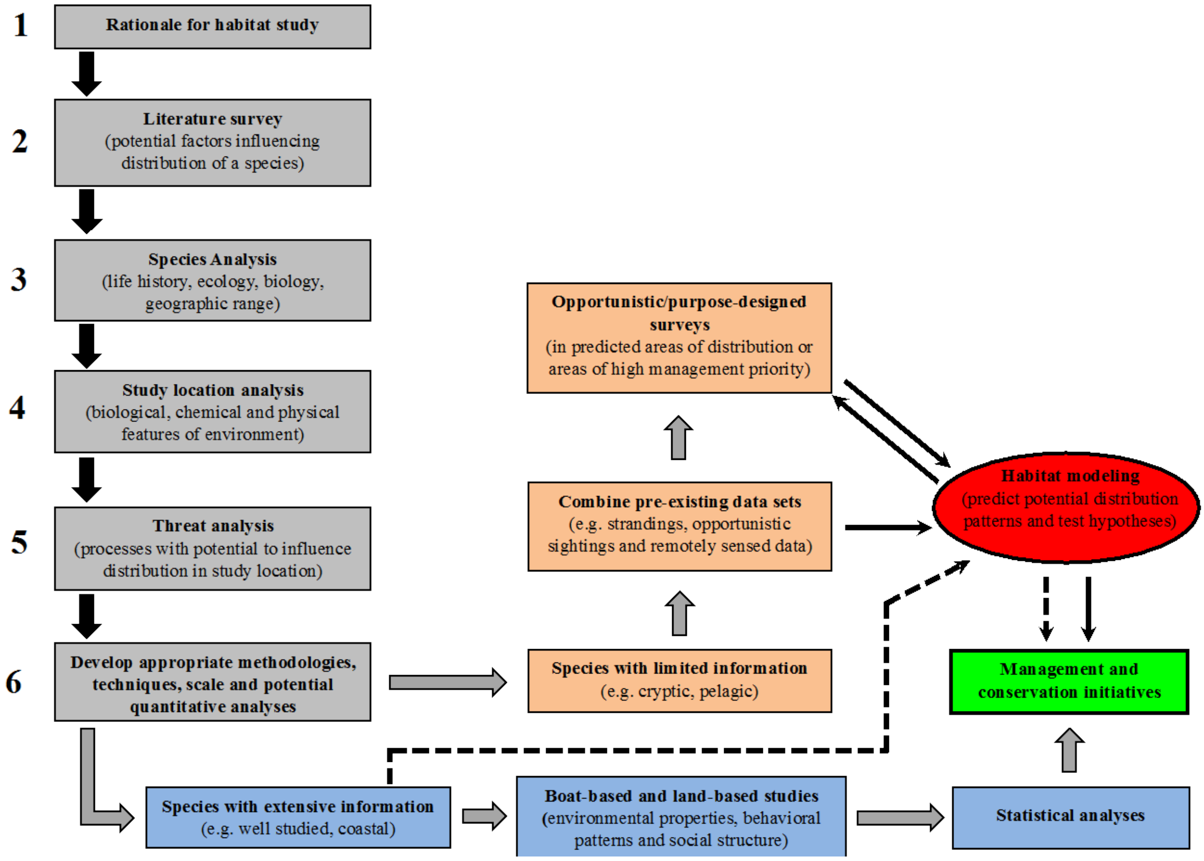


Figure 5. Logical flow chart diagram illustrating the proposed six recommendations on how future studies may become more targeted and effective in defining and describing cetacean habitat, noticeably through distinct strategies based on the status of the species in considerations, *i.e.* species with extensive information and/or ease of access (e.g. coastal, ubiquitous and abundant species) and species with limited information and/or difficult to study (e.g. cryptic, rare and offshore species).

thic characteristics, exposed vs. sheltered waters). These environmental features were then incorporated into the study as each was considered to have the potential to influence dolphin presence in this area.

Similarly, [38] aimed to define critical use areas for bottlenose dolphins (*Tursiops truncatus*) in the Shannon estuary, Ireland, with the intention to assist management plans for a candidate Special Area of Conservation. Specific knowledge of the habitat characteristics of dolphins in this area was therefore considered crucial in developing a management strategy. In particular, the locations of dolphin encounters, were used to identify specific areas of high use, as well as any preference for areas with particular topographic features, such as depth and benthic slope. Areas identified as high use by the dolphins were then deemed "critical areas", and therefore considered to be essential to the dolphins inhabiting the estuary.

5.2. Identify Potential Influencing Factors from the Literature

It is critical to identify the potential factors influencing cetacean distribution, such as environmental characteristics, that have previously been identified, as well as the research methodologies that were used to do so. In some instances, there may already be considerable knowledge available. For example, numerous global studies have documented resting spinner dolphin (*Stenella* sp.) populations showing strong site fidelity within specific bays and reefs during daytime [55]-[57]. These studies demonstrate the consistent use of resting areas which have specific and common environmental features such as shallow, sheltered tropical bays or lagoons with sandy bottoms [58]. The identification of key environmental features provides a basis and direction in which to start the development of a habitat approach and identify the reasoning behind why these specific locations are utilized and others are not. In contrast, for those rarely sighted and data deficient species, information or potential habitat factors may be significantly lacking. In some cases only broad distribution ranges noted by a species synopsis or report may be available [5] [59]. This paucity of information can initially hinder the development of a habitat approach. However, general information about specific oceanographic occurrences or the oceanic waters within an animal's broad distribution presumed range may offer some place in which to start thinking about influencing habitat factors. Ultimately, the findings and level of information available from this type of review will assist to structure the scale and range of focus of the study.

5.3. Species Analysis

An essential part in approaching habitat is an assessment of the life history, ecology and biology of the species in question. Therefore species need to be considered on an individual basis. Factors such as geographic range, distribution, motion behavior and migrational patterns, home range and site fidelity need to be incorporated into the study. For rarely encountered and cryptic species, information may be limited or difficult to obtain. For example, insights into the biology, geographic range and distribution of species such as the beaked whales (family Ziphiidae) have often only been established through brief encounters and stranding occurrences [60]. This paucity about a species biological and ecological requirements allows us to then only assume those potential important factors such as geographic range. In contrast, we know a lot about some species specific movement patterns such as the Southern right whale (*Eubalaena australis*). Populations of this species annually migrate in the austral winter from southern Antarctic feeding grounds to sheltered waters on the Southern Australian coastline for calving [61]. The occurrence of these migration events, therefore allows a more systematic approach to be taken, as we can predict where these animals are going to occur at certain times of the year. Furthermore, we can also potentially assume their use of these areas, for example for calving.

In addition, the differing life strategies and diurnal behavioral patterns should also be considered [7]. A species life history can potentially provide insight into surrounding environmental features, as adaptations are potentially linked and influenced by it [62]. Possible inclusions for this review might include: feeding strategies, calving intervals, resting patterns and group size. In this context, spinner dolphins (*Stenella* sp.), are considered to have a unique life history strategy, in that some populations rest during daylight hours and feed offshore at night in the mesopelgic zone [63]. Similarly, bottlenose dolphins (*Tursiops* sp.) often engage in location specific foraging tactics and techniques (e.g. [64]-[66]).

5.4. Location Analysis

An analysis of the potential study location needs to be conducted to identify what environmental factors present in the area should be addressed. More specifically, the general nature of the study area's physical features/properties needs to be identified, e.g. estuary, gulf, bay or reef, exposed open ocean vs. sheltered waters. In addition, the topography, bathymetry, substrate type and the presence of islands, reefs, submarine canyons and ice cover within the environment should also be considered as potentially influencing habitat factors. Once the key features of the environment have been identified, those obvious oceanographic features and phenomena, specific to the area can then be included into the assessment. For example, water temperature, depth, salinity, turbidity, the presence and depth of a thermocline, current direction and intensity, eddies, current flow, upwelling events, primary productivity and the seasonal fluctuations of these environmental characteristics. Additionally, anthropogenic presence, predation pressure and resource availability need to be considered.

In this context, a variety of environment types had been noted to occur within the Adelaide Dolphin Sanctuary, South Australia [67]. Preliminary investigations indicated that bottlenose dolphins were frequently sighted utilizing specific areas within these different environment types. The sanctuary contained 2 distinctly different physical environments (e.g. open waters with seagrass beds and shallow, sheltered waters with bare, sandy substrate) which also potentially caused variations in the oceanographic occurrences. Therefore, within the current study plan the physical environmental features and oceanographic parameters (including seagrass presence, sheltered estuarine versus exposed gulf waters, water temperature, depth, salinity, turbidity and dissolved oxygen) considered to influence dolphin presence the most, or be important to specific life history strategies (e.g. feeding, calving) were taken into consideration as part of the survey plan. This inclusion of a wide spectrum of physical, chemical and biological environmental features such as these listed above will therefore enable a thorough investigation into those abiotic and biotic potential habitat drivers.

5.5. Threat Analysis

Additional factors and threats present in the marine environment should also be considered within the development of a comprehensive habitat approach. This inclusion will assist in identifying whether the presence of a threatening process drives the animal's distribution. Ultimately, this will influence how habitat is described. A study investigating the influence of repeated vessel exposure on a resident population of bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia, then suggested that over time the repeated presence of vessels potentially could affect dolphin abundance, and as a result the habitat used [34]. Although this study did not specifically focus upon describing habitat, it demonstrated how anthropogenic impacts can potentially shift or alter the way animals distribute themselves within their surrounding environment if exposed to threats. Similarly, biological threats such as the predation of sharks also have the potential to influence distribution and ultimately the habitat used [31]. Therefore, threats to potentially include in a habitat approach are those that have the potential to affect and alter distribution. Impacts such as predator presence, pollution, drives hunts, tourism activities, commercial and artisanal hunting, fisheries, habitat degradation and climate change effects (e.g. water temperature change over time, receding ice cover) could be considered to impact distribution on an immediate, short-term or long-term level.

5.6. Developing Appropriate Methodologies and Techniques

The five previous considerations discussed above have identified context (in terms of objectives, species and location) and a list of factors, which should be considered within the development of a sound and objective approach to researching and studying cetacean habitat. This background information enables the selected factors to be appropriately adapted in terms of spatial and temporal scale, species biology, region and current threats. When combined with the appropriate methodologies and techniques the information gained will provide a more detailed synoptic assessment of cetacean habitat, which is therefore more targeted and applicable to potential management initiatives. However, it is considered that the suitable combination of these will ultimately begin to provide an initial insight into any potential animal and environmental relationships. Currently, many methodologies, techniques and quantitative analyses (e.g. [2] [68]-[71]) are available for application within cetacean specific research. However, these can be incorporated within a cetacean habitat approach.

In this context, the following are innovative examples of some of the ways in which cetacean habitat studies could be progressed and techniques implemented. However, this approach is not limited to these, and they are provided for illustrative purposes. The focus and implementation of methodologies and technologies will differ according to the logistics of the study location (e.g. coastal vs. offshore). Currently, many have been developed to assist in overcoming logistics, particularly when investigating cetaceans in the open ocean. For example, modern technologies such as remote sensing imagery, Argo floats, gliders and animal borne sensors (e.g. [32] [72]-[75]) can provide some information about the biogeographical range of cetaceans as well as open new perspectives into a detailed understanding of the vertical structure of the water column (**Figure 6**). When coupled with distribution patterns, for example, this oceanographic information could be used to provide insights into the potential mechanisms linking ocean processes, whales and their prey [76] [77].

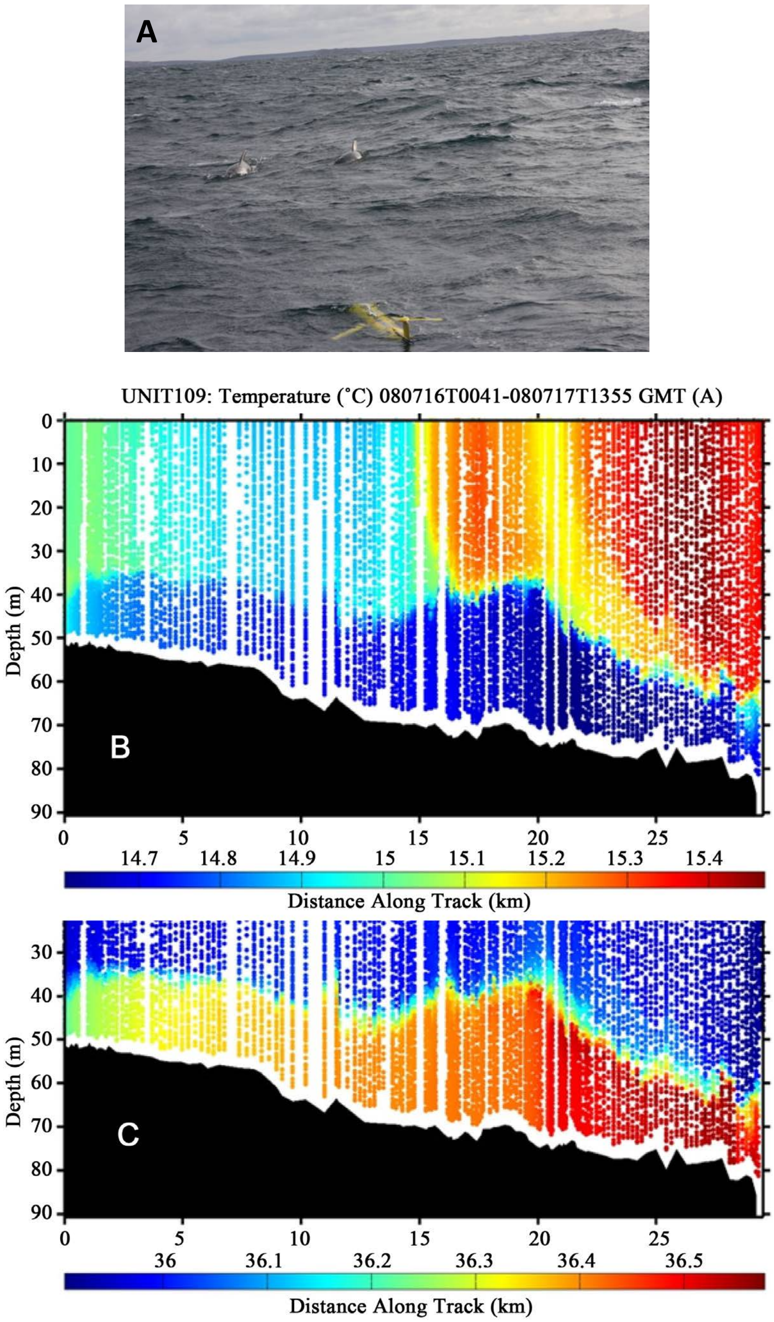


Figure 6. Modern technologies, here a Sloccum gliders deployed off Kangaroo Island (South Australia) being escorted by two bottlenose dolphins (*Tursiops* sp.; (A)), have the potential to assist in the collection of valuable cetacean habitat data, such as high-resolution temperature (B) and salinity (C) structures. Image credit: South Australian Marine Integrated Observing System, SAIMOS [75].

In addition, oceanographic information has also the potential to complement data collected through opportunistic sightings, or help to correlate sighting locations, particularly for rarely sighted offshore and deep diving species. More specifically, this information may be useful, particularly for species, spending majority of their time for example, below the surface feeding such as sperm whales (*Physeter microcephalus*; [78]). Furthermore, as well as providing information about potential habitat correlations, these technologies can offer some insight into behavioral patterns. For example, [74] investigated the movement patterns of Blainville's beaked whales (*Mesoplodon densirostris*) off the coast of Hawaii using Argos-linked satellite tags. Additionally, the use of such methodologies and technologies in conjunction with *in situ* measurements, correlated with behavioural and social structure data can also potentially start to provide insight into cetacean ecology and life histories.

It is also stressed that the use of technologies in the field may also be complemented by, baseline cetacean habitat information gathered through the application of pre-existing data sets, particularly those gathered long term. When complemented with oceanographic information, gathered through the use of technologies or *in situ*, these have the potential to be of benefit to pre-existing data sets consisting of cetacean sightings and distribution patterns [79] [80]. Additionally, pre-existing data sets of species specific distributions have the potential to provide much insight into distribution in the way of being used as predictor tools for distribution (e.g. [2] [71] [81]), which ultimately can help focus a study for a specific species or location. Additionally, these can now be combined with freely accessed oceanographic datasets through ocean portals, therefore it is possible to conduct preliminary studies based on all pre-existing data.

6. Conclusion

Given the difficulty and complexity of adequately understanding the meaning of habitat for cetaceans, the development of a sound approach incorporating suitable techniques and methodologies is critical to enable the quantification of appropriate variables. Understanding the influences and the inter-relationships between cetaceans and their surrounding environment will not only greatly improve our understanding, but also ultimately allow us the ability to develop targeted and more effective mitigation and conservation measures.

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