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Ecological bridges and barriers in pelagic ecosystems

Dana K. Briscoe[a]
Alistair J. Hobday[b]
Aaron Carlisle[a]
Kylie Scales[c]
J. Paige Eveson[b]
Haritz Arrizabalaga[d]
Jean Noel Druon[e]
Jean-Marc Fromentin[7]

a. Stanford University, Hopkins Marine Station, Pacific Grove, CA 93950, USA
b. CSIRO Oceans and Atmosphere, Hobart, Tasmania, 7000, Australia
c. Environmental Research Division, Southwest Fisheries Science Center, National Oceanic and Atmospheric Administration, Monterey, CA 93940, USA
d. AZTI, Marine Research Division, Herrera Kaia Portualdea z/g, 20110 Pasaia, Basque Country, Spain
e. European Commission, Joint Research Centre (JRC), Institute for the Protection and Security of the Citizen (IPSC), Maritime Affairs Unit, Via Enrico Fermi 1, 21027 Ispra VA, Italy
f. IFREMER, UMR MARBEC - Marine Biodiversity, Exploitation & Conservation, Avenue Jean Monnet, CS 30171, 34203 Sète Cedex, France

Abstract

Many highly mobile species are known to use persistent pathways or corridors to move between habitat patches in which conditions are favorable for particular activities, such as breeding or foraging. In the marine realm, environmental variability can lead to the development of temporary periods of anomalous oceanographic conditions that can connect individuals to areas of habitat outside a population’s usual range, or alternatively, restrict individuals from areas usually within their range, thus acting as *ecological bridges* or *ecological barriers*. These temporary features can result in novel or irregular trophic interactions and changes in population spatial dynamics, and, therefore, may have significant implications for management of marine ecosystems. Here, we provide evidence of ecological bridges and barriers in different ocean regions, drawing upon five case studies in which particular oceanographic conditions have facilitated or restricted the movements of individuals from highly migratory species. We discuss the potential population-level significance of ecological bridges and barriers, with respect to the life history characteristics of different species, and inter- and intra-population variability in habitat use. Finally, we summarize the persistence of bridge dynamics with time, our ability to monitor bridges and barriers in a changing climate, and implications for forecasting future climate-mediated ecosystem change.

Key words: species distribution, migration corridors, population connectivity, oceanographic features, tuna, billfish, marine mammal, Brazilian episode

1. Introduction

Throughout the biosphere and across all scales of ecological organization, the environmental conditions that constitute animal habitats are arranged in a complex, hierarchical and heterogeneous configuration. This patchiness can restrict sessile animals to the same habitat 'patch' for most of their lifetime while mobile animals can move between suitable patches, because they can tolerate unfavorable conditions when moving between preferred habitats (Switzer, 1993). These movements across a landscape or seascape connect populations and allow for life history processes that are essential to population persistence (Gilbert-Norton et al., 2010) and ecosystem function (e.g. genetic flow, nutrient cycling, Reimchen et al. (2003); Sanchez-Pinero and Polis (2000)).

Habitat connectivity – the degree of interconnectivity between patches of favorable habitat – is essential, not only for individual survival but also for the maintenance of metapopulation structure, and ultimately, biological diversity (Hanski, 1999). Seasonal events may trigger dispersal or migration to exploit different habitats that are beneficial to reproduction and fitness (Dingle, 2009; Murrell et al., 2002). In terrestrial landscapes, many large-bodied ungulates and winged species undergo lengthy migrations (Harris et al., 2009), avoiding unsuitable habitats, crossing barriers or temporarily tolerating unsuitable environments (e.g. wildebeest in Serengeti (Ottichilo et al., 2001) and raptor migrations across Sahara (Strandberg et al., 2009)).

In marine systems, satellite-tracking studies of pelagic fishes, sea turtles, seabirds and marine mammals have shown impressive transoceanic migrations between areas used for different stages of the ontogenetic or annual cycle (Akesson and Hedenstrom, 2007; Block et al., 2011; Bonfil et al., 2005; Scott and Hays, 2014; Shaffer et al., 2006). The routes that characterize movement between suitable habitats and that are spatially persistent are known as corridors (Anderson et al., 2013; Beier and Noss, 1998; Bennett, 1999). While habitat corridors in terrestrial environments are well understood (e.g. monarch butterflies (Brower, 1995); osprey (Alerstam et al., 2006)), the concept of corridors in the marine realm is less developed. Yet highly mobile marine species are also known to utilize seasonally dynamic oceanographic features to move between known breeding and foraging habitats (Guilford et al., 2009; Morreale et al., 1996; Polovina et al., 2006). Some corridors are well defined by the seasonal or annual predictability of a population returning generation after generation (Anderson et al., 2013).

There are also locations within a species range that have periodic bouts of anomalous environmental conditions that may influence habitat suitability. In pelagic systems, currents and mesoscale oceanographic features (e.g. eddies, fronts, filaments, changes in vertical mixing) are the major sources of this environmental variability over intra-annual timescales (Bakun, 2006). In contrast to predictable and regularly used migratory corridors, anomalous environmental conditions may lead to the development of short-lived corridors or *ecological bridges*. Following Fromentin et al. (2014a), we define an ecological bridge as a temporary habitat pathway connecting two suitable but distinct habitat region*s* (Fig. 1). Anomalous oceanographic conditions and changes in mesoscale variability can create such ecological bridges, and allow individuals access to alternate, or irregular, areas of habitat. We distinguish this from cases where a single habitat expands to new regions thereby allowing species to increase their range (e.g. Mackenzie et al., 2014; Stewart et al., 2014), which has been increasingly observed as ecosystems respond to global climate change (Hollowed et al., 2013; Kirby et al., 2006).

In contrast to ecological bridges, migrating animals are often confronted with barriers between favorable habitat patches. Ecological barriers can be geographic (e.g. seas, land masses, deserts, or mountains), or environmental (e.g. temperature and salinity gradients, light or oxygen levels, (Prince and Goodyear, 2006; Selkoe et al., 2008). Profound changes to corridors and barriers have occurred in the past, e.g. historical episodes of climate change and tectonic activity (Gaston, 2003). Some change more quickly, in synchrony with timing and intensity of interannual and decadal events (ENSO and PDO) (Lehodey et al., 1997; Massom and Stammerjohn, 2010).

The timing and location of ecological bridges and barriers may change over space and time, connecting (or disconnecting) animals to disjunct (or adjunct) habitats, with a range of ecological implications. Here we provide evidence of ecological bridges and barriers in the marine realm, drawing upon case studies in which a particular set of oceanographic conditions have facilitated or prevented the movements of individuals between patches of favourable habitat. In Section 2, we present five case studies of ecological bridges and barriers, detailing how each bridge (barrier) is formed and how species respond, how the presence of a bridge (barrier) affects population structure and connectivity, and the socio-economic implications (if any). We then generalise the importance of bridges and barriers in terms of dynamics, population level significance, and future research needs (Section 3).

2. Ecological bridges and barriers in pelagic systems

The movements and migratory patterns of pelagic species can have important ecological and population level effects (Dingle, 2014; Frisk et al., 2014), especially in higher trophic level predators which can play an important role in structuring and maintaining marine food webs (Heithaus et al., 2008). While both physical and biological factors influence the movements and resulting patterns in population structure and connectivity in marine species (Frisk et al., 2014), we mostly focus here on changes in the physical environment. Case studies from pelagic fishes and marine mammals demonstrate how shifting environmental conditions create ecological bridges or barriers that can influence the distribution of migratory marine species with potentially important ecological effects at the population level, as described below.

2.1 Atlantic bluefin tuna: the Brazilian episode and a bridge between two hemispheres

Throughout its thousand years of exploitation, catches of Atlantic bluefin tuna (ABFT, *Thunnus thynnus*) have exhibited conspicuous changes in both time and space domains (Fromentin et al., 2014a; Mather et al., 1995; Ravier and Fromentin, 2004), probably reflecting the high mobility of the species (Block et al., 2005; Sibert et al., 2006). During the 20th century, large Nordic and Japanese fisheries rapidly arose in unexpected fishing areas, i.e. the North and Norwegian Seas and the equatorial Atlantic, but suddenly disappeared after a few years or decades. Those variations seem to be primarily due to environmentally driven changes in ABFT migration patterns that could act in synergy with local/regional overfishing (Fromentin, 2009).

One of the most striking changes in ABFT spatial distribution was the so-called "Brazilian episode", during which Japanese longline fishing boats caught large quantities of ABFT (a temperate species) in the equatorial Atlantic where they were targeting tropical tunas (Fromentin et al., 2014a; Takeuchi et al., 2009). In a study by Fromentin et al. (2014a), a niche model was applied to an extensive dataset of catch and environmental variables from 1960 to 2009. Results showed that ABFT has a remarkably large ecological niche, with high probabilities of occurrence in the North Atlantic and adjacent seas (as expected), as well as in the South Atlantic at around 30°S and along the southwestern African coast (Fig. 2a). The niche model also detected favorable environmental conditions for ABFT in the western equatorial Atlantic during the 1960s, exactly where the Japanese vessels caught ABFT. The 1960s were the only decade in the last 50 years that exhibited relatively high probability of ABFT occurrence around the Equator. No ABFT have been caught in the equatorial Atlantic since then, although the fishing effort significantly increased in that area. During the last decade, higher probabilities of ABFT mostly occurred above 45°N (Fig. 2b), which could be related to global warming and which agrees with a northward expansion of ABFT (see below). ABFT could have thus migrated from their northern spawning grounds to the South Atlantic during the 1960s through the western equatorial Atlantic acting as an ecological bridge between the central North and the central South Atlantic. These new geographical spots could have subsequently been transmitted from year-to-year through spatial learning and entrainment of younger fish (Petitgas et al., 2010).

Further analyses indicated that during that period, ABFT could have migrated from the equatorial Atlantic to the western spawning ground of the Gulf of Mexico during the first part of the year followed by a reverse north-south migration during the second part of the year (Fromentin et al., 2014a). The southeastern Atlantic feeding grounds (offshore of South Africa, Namibia and Angola) may well have been shared by both ABFT and southern bluefin tuna during the 1960s. However, this bridge appears to have broken by the late 1960s because of oceanographic changes affecting primarily sea surface temperature and possibly the equatorial current and counter-current. This could have made ABFT migration to the South Atlantic more difficult. ABFT has high rates of natal homing (Rooker et al., 2008) and as connections have been detected between the western equatorial Atlantic and the Gulf of Mexico, but not with the Mediterranean Sea, it is highly probable that those individuals were part of the western Atlantic ABFT stock. Therefore, the breaking of this ecological bridge may have primarily affected the productivity of the western stock and its lack of rebuilding could result from a regime shift due to the combination of oceanographic changes in the equatorial Atlantic (the breaking of the ecological bridge) and intense fishing in the North Atlantic in the 1960s-1970s (Fromentin et al., 2014a).

Because ABFT displays a large ecological niche, it has potentially more abiotic opportunities (i.e. a larger ecological window) than many other large pelagic fish. This may explain why the ABFT spatial distribution appears generally highly variable. The ABFT spatial distribution seems to have expanded northward (beyond 50°N) in the last decade (as it did from the 1930s to the 1950s), probably because of the effects of global climate change. This is particularly evident in the western Atlantic, with the northern expansion of large ABFT in the Gulf of Saint Lawrence. MacKenzie et al. (2014) postulated that the presence of bluefin tuna in waters east of Greenland in 2012 could be due to a combination of warmer temperatures and immigration of an important prey species (mackerel) to the region, indicating that global warming will open (or close) ecological bridges in the northern (southern) parts of the oceans to marine fish and, probably to other marine vertebrates.

2.2 Atlantic bluefin tuna: the western pulse into the Bay of Biscay

In the Northeast Atlantic, the Bay of Biscay is a key juvenile ABFT feeding ground. Juveniles migrate into the Bay of Biscay in April-June, where they feed on the abundant local prey and grow before migrating back to Atlantic wintering areas in autumn (Dufour et al., 2010). Some adults also feed in the Bay of Biscay after spawning in the Mediterranean (Aranda et al., 2013). Using different technologies (such as conventional tags, electronic tags, or chemical tags), Bay of Biscay ABFT have been shown to be substantially connected with other areas across the Mediterranean and the western Atlantic (Abascal et al., 2016; Arregui et al., 2006; Graves et al., 2015). However, the natal origin of Bay of Biscay ABFT remained unknown until the otolith chemistry study by Fraile et al. (2015). Using a substantial sample of juveniles and adults over three consecutive years, they found that the Bay of Biscay is supported almost exclusively by the eastern ABFT population, but the western population may also occasionally contribute in some years. Given that the eastern population is believed to be an order of magnitude larger than the western population (Kerr et al., 2015), ABFT of western origin is particularly difficult to detect in eastern foraging areas. In fact, a small proportion of western migrants was detected in the Bay of Biscay only in 2009 – a western pulse. In contrast, the Bay of Biscay fishery was composed exclusively of eastern origin bluefin tuna in 2010 and 2011. Based on their sampling, Fraile et al. (2015) suggested that a substantial fraction of the western population may move across the Atlantic Ocean to feed in the Bay of Biscay and/or surrounding waters of the Northeast Atlantic.

Across the three consecutive fishing seasons, all the western origin ABFT detected in the Bay of Biscay were caught within a very restricted time window (10 days) in 2009, suggesting high temporal variability in the transatlantic migration from west to east, with migration events occurring in sporadic pulses that could be related to variability in environmental conditions (Fraile et al., 2015). A recently developed habitat model that notably includes productive mesoscale features as a proxy for food availability (Druon et al., 2016) suggests that the 2009 pulse of western origin ABFT into the Bay of Biscay might have been due to the existence of a longitudinal ecological bridge across the Atlantic (Fig. 3a). One to three months prior to sampling in 2009, this habitat bridge which is linked to the Gulf Stream dynamics connected the main western and eastern Atlantic feeding areas through a well-defined, relatively narrow corridor west of 45ºW. During the ABFT migration period to northeast Atlantic feeding grounds after wintering (from April to June), the potential feeding habitat in the central part of the bridge was observed to be largest in 2009 compared to 2010 and 2011 (Fig. 3d). The bridge between the eastern and western feeding areas in 2010 and 2011 was less marked and more discontinuous, which might have acted as a barrier against migration of western origin ABFT into the eastern Atlantic feeding grounds (Fig. 3b and c).

Mixing of eastern and western ABFT across the whole Atlantic Ocean remains one of the most critical uncertainties preventing accurate diagnoses of stock status to guide effective management (Fromentin et al., 2014b). Different studies have illustrated the complexity of the connectivity between remote Atlantic areas and their implications for ABFT management (Block et al., 2005; Galuardi and Lutcavage, 2012; Rooker et al., 2014;

Rooker et al., 2008). Effective fishery management will require a better understanding of the magnitude of these movements, their temporal variability, and the physical and biological factors that may affect it (Graves et al., 2015).

More research is needed to better understand the role of habitat bridges and barriers in relation to ABFT population connectivity. If bridges are not persistent over time as driven by climate change over the Gulf Stream dynamics, western origin ABFT that migrated into the eastern Atlantic might be less likely to return to the west (and vice versa for the eastern origin population to the east). Depending on the magnitude of such potential habitat barriers preventing the migration back to the west, important implications could include exposure to potentially higher fishing intensity, or delays in the natal homing behavior to spawn in the Gulf of Mexico (and vice versa in the Mediterranean Sea for the eastern origin population). The monitoring of these habitat contraction and relaxation acting as barriers and bridges under climate change is therefore essential to evaluate the important potential implications for ABFT population connectivity and dynamics.

2.3 Southern bluefin tuna: pathways to southeast Australia

Migration pathways of southern bluefin tuna (SBT *Thunnus maccoyii*) have been studied over many decades with conventional, acoustic, archival and satellite tagging programs, providing a range of insights into their movement and behaviour (Bestley et al., 2009; Fujioka et al., 2010; Hobday et al., 2015; Patterson et al., 2008). After hatching, fish move from the single-known spawning ground between Indonesia and Australia, following the Leeuwin Current down the Australian west coast to reach the southern coast by age 1. They are then resident during the austral summers in the Great Australia Bight (GAB) between the ages of 2-5 years. At the end of each summer, juvenile SBT leave the GAB and move east to the Tasman Sea or west to the Indian Ocean where they spend the winter feeding (Bestley et al., 2009).

A possible ecological bridge connecting juvenile SBT habitats was interrupted in the early 2000s, when eastward migration to the Tasman Sea became rare. Conventional tag-recapture data revealed that fewer juvenile SBT tagged in the 2000s moved into the Tasman Sea compared to fish tagged in the 1990s (Basson et al., 2012). Based on thousands of tag returns from SBT tagged at ages 1 and 2, the percent of returns coming from the Tasman Sea was much higher in the 1990s (5.7% and 12.8% for age 1 and 2 respectively) than in the 2000s (1% and 0.4% for age 1 and 2, respectively). Archival tag tracks also provide evidence for reduced eastward movement of juvenile SBT in the 2000s (Basson et al., 2012). Only 4% of tracks (3 out of 75) showed movement into the Tasman Sea (>150°E) during the months of May through November after 2001, compared to 21% (14 out of 67) in prior years (chi-squared test p-value=0.01). The exact timing of this change is difficult to determine as few tags returned data between 2001 and 2004.

These migration pathway changes may be in response to population decline (there has been a documented decline in SBT abundance and recruitment through the 1990s and into the 2000s, and cohorts in 2000-2002 were at historically low levels (Anon, 2009)), or to environmental changes that affect SBT migration. In the Tasman Sea, a long-term warming trend has been observed (Hobday and Pecl, 2014; Ridgway, 2007). Other areas occupied by juvenile SBT, such as the GAB and eastern Indian Ocean have not warmed as rapidly over the same period (Basson et al., 2012; Hobday and Pecl, 2014). This warming may be acting as a partial barrier to restrict juvenile SBT movements to areas they occupied in the 1990s.

Habitat models for juvenile SBT have been developed using location data collected on SBT over many years from electronic tags, and comparing the ocean conditions where fish were found with the conditions available to them throughout the region and time period of interest (Basson et al., 2012; Eveson et al., 2014). Sea surface temperature (SST) and chlorophyll were found to have the greatest influence. Habitat models based on SBT preferences for SST and chlorophyll revealed a high preference habitat band in April to June along the west and south coasts of Tasmania into the Tasman Sea in the period 1998-2000 that was no longer present in the period 2004-2006 (Basson et al., 2012). The habitat models have subsequently been updated to include new archival tag data and to use improved fish location estimates based on a recently published method for light-based geolocation (Basson et al., 2016). These updated models continue to show the disappearance of a connecting habitat band between the GAB and the Tasman Sea between the two time periods (Fig. 4). We note that separate habitat models were used for the two time periods since habitat preferences for SBT changed slightly between these periods (Fig. 4a,b). If we use a single habitat model based on the entire period 1998-2006, the missing band of suitable habitat in 2004-2006 is still evident but less extreme. We argue it is more defensible to use separate habitat models than to combine all years into a single model that masks the preference change. This does, however, raise the dilemma of whether the observed ecological barrier has arisen due to changes in fish physiology and behaviour or to environmental changes – most likely a combination of both. Changes in additional variables, such as forage distribution, remain difficult to estimate, and the habitat model remains a proxy for environmental change that restricted movements of juvenile SBT across this ecological bridge.

This example of an ecological bridge “breaking” foreshadows changes that are expected under climate change as environmental tolerances are exceeded in some regions (Burrows et al., 2014). If the ecological barrier persists, the implications for SBT populations are likely to be relatively minor, as this region is only a small part of their total range and larger SBT may not be restricted by the barrier. Dependent fisheries in eastern Australia and New Zealand may experience declines in catch, however, we are unable to estimate these effects. A new archival tagging program in the GAB commenced in 2015, and in a few years will allow new estimates of east-west migration and assessment of the state of this ecological bridge.

2.4 Blue marlin: intermittent crossing of the Equatorial Pacific

Like bluefin tuna, blue marlin (*Makaira nigricans*) is a wide-ranging species, with some of the most impressive long-range movements ever recorded for oceanic fishes (Kraus et al., 2011; Ortiz et al., 2003). In the North Pacific, 59 marlin were tracked from 2009-2013 moving south from Hawaii, crossing the equator and moving towards French Polynesia (Fig. 5). For most migratory species, the equator serves as a natural ecological barrier (e.g. see ABFT example above), due to the combination of high sea-surface temperature and oxygen limits at relatively shallow depths (MacLeod, 2009). However, in a recent study blue marlin were shown to routinely undergo a unique, trans-equatorial migratory strategy (Carlisle et al., In Press).

Interestingly, this trans-equatorial route was not used by blue marlin in 2010, perhaps due to a La Nina event. This cold phase of the ENSO cycle, which in the North Pacific is characterized by a western extension of the cool SST water mass from the eastern Pacific (cool tongue), increased equatorial upwelling and shoaling of the thermocline and oxycline (Philander, 1989; Wyrtki, 1975). Blue marlin tagged in 2010 moved south as they did during other years until they encountered the western extension of the cool tongue (Fig. 5b), which had water temperatures below 24ºC, below their preferred thermal range of 26 to 30°C (Goodyear et al., 2008; Graves et al., 2001; Holland et al., 1990). Upon encountering the cool tongue, the blue marlin stopped moving south and remained in the warm waters to the north of this cold oceanographic feature, with several fish moving longitudinally along its northern boundary. These cold temperatures, combined with the increased vertical habitat compression associated with shoaling of cold, low oxygen waters driven by increased equatorial upwelling, appeared to present a vertical and horizontal ecological barrier to trans-equatorial movements. During non-La Niña years, this oceanographic barrier to trans-equatorial migration is not present as SSTs are not limiting (Fig. 5a) and vertical habitat compression is reduced.

The effect on the population dynamics of blue marlin will depend on the extent and persistence of the barrier as well as the nature of the trans-equatorial migration. The purpose of the trans-equatorial migrations of blue marlin remains unclear, but in general the broad-scale migratory patterns of blue marlin have been linked to foraging and reproductive migrations (Shimose et al., 2009; Shimose et al., 2012). Hawaii is a known spawning location (Hopper, 1990; Seki et al., 2002), and French Polynesia has also been identified as a region where spawning occurs (Howard and Ueyangi, 1965). Hence, trans-equatorial movements may be related to spawning and disruption of these potential spawning migrations may have important effects in terms of population connectivity. In addition, reduced mixing rates between different populations may increase susceptibility of blue marlin to localized depletion due to overfishing (Lee et al., 2014). Much remains unclear about how oceanographic conditions will be altered under future climate change, but some research suggests that there will be an increase in the frequency of extreme El Niño and La Niña events (Cai et al., 2014; Cai et al., 2015; Power et al., 2013). Any increase in the intensity or frequency of La Niña events will likely increase the extent and persistence of such barriers, potentially dividing the population of blue marlin in the Central Pacific.

2.5 Bowhead whales: traversing the Northwest Passage

The Northwest Passage (NWP) is a series of Arctic waterways connecting the Atlantic and Pacific Oceans. Throughout most of the year, dense ice cover within the NWP represents a physical barrier between the two oceans (McKeon et al., 2015). Arctic species are well adapted to such barriers, and have tuned their feeding and breeding behaviors to coincide with seasonal changes in ice pack. Bowhead whales (*Balaena mysticetus*) are the largest Arctic predator, with a wide-ranging distribution and populations found on both sides of the NWP. The species is well suited for ice-covered waters, given their ability to move through extensive areas of sea ice coverage (Citta et al., 2015; George et al., 1989; Heide-Jørgensen et al., 2012; Laidre et al., 2008). Individuals spend the summer months foraging in Arctic waters and then migrate to subarctic seas during the winter months (Laidre et al., 2008).

While genetic evidence indicates historic gene flow between Atlantic and Pacific populations (Alter et al., 2012), the lack of bowhead remains from interior locations in the NWP suggests that individuals have maintained separate populations (McKeon et al., 2015). However, in the summer of 2010, and following a long-term warming trend, the NWP was suitably free of ice to allow two individuals from separate populations to forage in the same region at the same time (Heide-Jørgensen et al., 2012; McKeon et al., 2015). Individuals migrated back to their respective oceans after ten days. However, this short occupation of common territory demonstrated the occurrence of an ecological bridge, through which bowhead whales were capable of inter-population exchange based on sea-ice conditions (Heide-Jørgensen et al., 2012; McKeon et al., 2015).

The extent and thickness of Arctic sea ice has continued to decrease at an alarming rate (McKeon et al., 2015), and the accelerated loss of sea ice will increase the ease and frequency with which marine species are able to move between the Pacific and Atlantic Ocean basins (Heide-Jørgensen et al., 2012). As such, the disappearance of long standing ice barriers and subsequent increased frequency of bridge conditions will have a dramatic impact on a range of Arctic species (McKeon et al. 2015). As the effects of climate-mediated ecosystem change are likely to be most pronounced in the Arctic in upcoming decades (Burrows et al., 2014; Moore and Huntington, 2008), it is perhaps not surprising that bridges and barriers will appear in this region. The dynamics of ice-melt and the effects on availability of preferred foraging habitats will see Arctic marine mammals and seabirds begin to explore novel areas (McKeon et al., 2015). At the same time, greater accessibility to humans (e.g. increased ship transport, oil exploration, and industrial fishing) may have serious ecological impacts for Arctic species (McKeon et al., 2015).

3. Importance of ecological bridges and barriers

The preceding examples illustrate that highly migratory pelagic species encounter ecological bridges and barriers that have facilitated or prevented individual movements over a range of space and time scales. In pelagic systems, the range over which individuals from a population tend to roam is an important consideration in the ability of those individuals to exploit an ecological bridge, or be restricted by an ecological barrier. The case studies presented here describe the movements of large teleost fish and marine mammals, which are among the most wide-ranging of all pelagic marine vertebrates (Block et al., 2011) and so most likely to encounter novel habitat conditions. Ecological bridges and barriers can modify spatial dynamics and connectivity of a population, impact on fisheries, and in the long term may affect population structure. For example, connectivity to new habitat may initiate conspecific interactions between separate populations, introduce new competition for resources, and modify existing biotic interactions and phenotypic traits (Brown et al., 2015). Below, we discuss the persistence in bridge dynamics with time, individual to population level sensitivity, and our ability to monitor bridges and barriers in a changing climate.

3.1 Bridge and barrier dynamics

Importantly, ecological bridges and barriers may support a complex meta-population structure and thus safeguard populations from local extinction events (e.g. hypoxic dead zones, corrosive waters), inter-annual variability (e.g. ENSO-related events, 'anomalous' years), and even unprecedented changes to oceans. As rapid climate change is expected to impact pelagic species (Dell et al., 2015; McBride et al., 2014; Robinson et al., 2015), the spatio-temporal dynamics of ecological bridges and barriers will be inherently linked to the periodicity and frequency of environmental and oceanographic variability in pelagic systems. In effect, the significance of ecological bridges and barriers will depend on the prevalence of environmental events and the life history stage at which an individual exploits a bridge or barrier.

For some of our case studies, the oceanographic drivers are unclear, but it is clear that bridge and barrier dynamics can be influenced on a range of time scales – for example, by decadal-scale cycles such as the El-Nino Southern Oscillation, the Pacific Decadal Oscillation and the North Atlantic Oscillation (Higuchi et al., 1999). In ocean regions where these climate drivers dominate, the biological responses may be influenced by the appearance of bridges and barriers every few years (e.g. blue marlin). If there is a change in the frequency of these climate modes (e.g. Table 1a), but no overall climate trend, then the periodicity of the ecological bridge or barrier may also be affected. An increase in the "breakdown" of the bridge conditions may lead to a decline in total population growth. Long-term changes in bridge appearance (either declining or increasing frequency) have occurred in the past, and are likely under climate change. Development of bridge permanence, such as might be occurring in the Arctic now (e.g. bowhead whale), may lead to loss of metapopulation structure if breeding between Atlantic and Pacific populations (Table 1b), while a declining bridge frequency or barrier permanence may lead to great population division and perhaps, over millennia, speciation (Table 1c). Ecological bridges may be transient features in a changing climate, with the appearance of the bridge linked to the rate of long-term change and the natural ocean variability.

3.2 Population-level significance

The significance of ecological bridges and barriers to pelagic species will likely be dependent upon aspects of that species' life history characteristics and the ontogenetic stage of individuals utilizing them. Important considerations include spatial range, distribution, fundamental niche width, fidelity to breeding or foraging areas, and the relative importance of proximate environmental influences versus learning and memory on at-sea space use. Scaling from individual movements to population-level significance, ecological bridges may be more readily exploited by neonate and juvenile stages of pelagic organisms, as they disperse away from sites of natal origin.

In addition to the extent of a population's space use, the width of the fundamental niche of a particular species may influence their propensity to use ecological bridges. A recent theoretical model (Mariani et al., 2016) suggests that habitat suitability, migration cost, and population structure can regulate habitat selection of highly migratory species. Our case studies describe the broad ecological niche of bluefin tuna, which are able to exploit a variety of prey types and tolerate a wide range of abiotic conditions (Arrizabalaga et al., 2015; Fromentin et al., 2014a), and so can expand into novel regions with ease. More specialised foragers, such as some surface-seizing and plunge-diving seabirds, require a particular set of biophysical conditions and availability of certain prey types for effective foraging, and so may be less likely to use ecological bridges in which conditions are not energetically favourable (Ancona et al., 2012). For many species, particularly marine ectotherms such as sea turtles, thermal sensitivity is a particularly important aspect that might influence the response to barriers or bridges (Hawkes et al., 2007; McMahon and Hays, 2006).

Moreover, fidelity to breeding and foraging habitats, and to migratory routes between these habitats, is important to consider when questioning how movements through ecological bridges might scale from individual- to population-level. A taxonomically diverse range of marine vertebrates are known to demonstrate fidelity to particular foraging or breeding habitats (e.g. tuna, Rooker et al. (2008); sharks, Queiroz et al. (2016); sea turtles, Broderick et al. (2007); seabirds, Weimerskirch (2007)). This implies a considerable influence on learning and memory in space use by a range of taxa (Regular et al., 2013).

Those that rely on learning and memory to navigate over proximate cues are less likely to expand their range into new regions through an ecological bridge (Carroll et al., 2015). For some fish species, it has been shown that the breakdown of information flow in a fish community can cause habitat contraction and drive stocks to collapse in certain regions (Petitgas et al., 2010) Moreover, theoretical analyses (Berdahl et al., 2016; De Luca et al., 2014) suggest that for species moving in large groups (i.e. schooling), group formation can be subject to threshold effects that alter migrations. For example, changes in individual preference and/or of the total population density can produce rapid alterations in group formation and collective behaviour to a point at which migration to other habitats may be stopped (De Luca et al., 2014). As a result, any consideration of range expansion or contraction must recognise the inherent interplay between an animal's responses to the contemporaneous environment and the intrinsic motivations that underlie movements and behaviours (Carroll et al., 2015).

In addition to species-specific constraints, ontogenetic stage may be important when considering the significance of ecological bridges. While large pelagic fish are most readily tagged, the movements of smaller juveniles and neonates may be of particular relevance to ecological bridges. Individuals in dispersive life stages are more likely to expand the population range into new habitats, as larval stages or neonates can often be advected in prevailing current flow (e.g. sea turtle hatchlings, Hays et al. (2010)), and juveniles are more likely to make exploratory movements at the edges of a population's current range (e.g. reef sharks, Chin et al. (2013); breeding colony prospecting in immature seabirds, Dittmann et al. (2005); Northern gannet on Farallon Islands, McKeon et al. (2015)). Conversely, individuals of breeding age may be less likely to exploit opportunities resulting from ecological bridges because many species show fidelity to particular breeding grounds, or natal philopatry (e.g. turtles, Luschi et al. (1998); whales, Wedekin et al. (2010); sharks, Feldheim et al. (2014); tuna, Block et al. (2005)).

The question of whether the significance of ecological bridges scales from changes in individual movements over intra- to inter-annual timescales to population-level effects remains unanswered. For some species, such as seabirds and marine mammals, that are now able to move through the ice-free Northwest Passage, this novel connectivity between habitats is almost certain to entail population-level effects, including genetic mixing, the establishment of new breeding colonies for seabirds, and possible population expansion into regions that marine mammals historically occupied but were extirpated. Thus, connectivity can contribute to meta-population recovery of historically over-exploited species, including various populations of marine mammals and bluefin tunas. This could improve the resilience and sustainability of tuna fisheries, provided both tuna populations and fisheries can adapt to novel spatio-temporal dynamics.

3.3 Future research

Advances in satellite telemetry and species distribution models have provided a wealth of information linking the movements and behaviors of highly migratory species to environmental conditions (e.g. Block et al. (2011); Hammerschlag et al. (2011); Hazen et al. (2013); Hobday et al. (2011)). Integration of these findings reveals the importance of spatio-temporal scales in understanding species-environment linkages (Hazen et al., 2013). Our case studies describe changes in migratory corridors, which may be particularly important in modifying the spatial dynamics of habitat use by populations of highly migratory species, affecting circumpolar, trans-equatorial and trans-oceanic species distributions. However, ecological bridges and barriers are likely to manifest over a range of spatio-temporal scales, and further research into the mechanisms of biophysical coupling in the pelagic ecosystem is necessary to truly understand the wider significance of these anomalous events. The examples presented here are based on tracking and habitat models, yet limitations still exist in our ability to track individuals throughout their life history stages and thus over the environmental conditions experienced over a lifetime. Such information, coupled with spatially explicit demographic models, may assist scientists and managers in developing predictions and projections of species' responses to anticipated environmental change (Dunning Jr et al., 1995).

While ecological bridges and barriers may be transient features in a changing climate, they can foreshadow changes that are expected under climate change as environmental tolerances are exceeded in some regions (Burrows et al., 2014). High-resolution climate predictions (e.g. Popova et al. (2016)), may add further understanding as to when, where, and how frequently bridges and barriers are likely to form over a variety of spatial and temporal scales. Together, such models can be used to simulate changing pelagic seascapes, providing management with scenarios to consider should an ecological bridge or barrier originate, decline, or persist.

3.6 Conclusions

Understanding changes in the marine environment continues to be challenging. Highly migratory species must navigate a fluid and shifting environment, adding complexity to how behavioral adaptations occur in relation to their immediate environment. Here, we have shown how ecological bridges and barriers can result in changes in highly mobile species distributions, population dynamics, and connectivity with their proximate environment. The availability of novel habitats through ecological bridges or disappearance of traditional habitats through ecological barriers may impact on a range of pelagic species. Important considerations include integration of life history characteristics and population-level sensitivity to their environment, as well as a greater awareness and understanding of the periodicity and frequency of bridges and barriers with time. As the effects of climate-mediated ecosystem change are likely to be even more pronounced in the coming decades (Burrows et al., 2014; Moore and Huntington, 2008), understanding how highly migratory species navigate a changing environment will be more important than ever.

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Table and Fig. Captions

Table 1. Schematic illustration of oceanic systems with bridge and barrier conditions over time. Shaded grey area indicates time periods when the periodicity has changed in A, and where bridges and barriers occur in B and C.

Fig. 1. (a) Examples of ecological bridges and barriers for five populations of pelagic species along their migratory routes (solid white line). Dashed lines represent individual movements upon the formation of a bridge (blue) or a barrier (red). (b) Schematic showing an ecological bridge connecting two ocean regions (time 2; dashed circle) that were not connected before (time 1) or after (time 3).

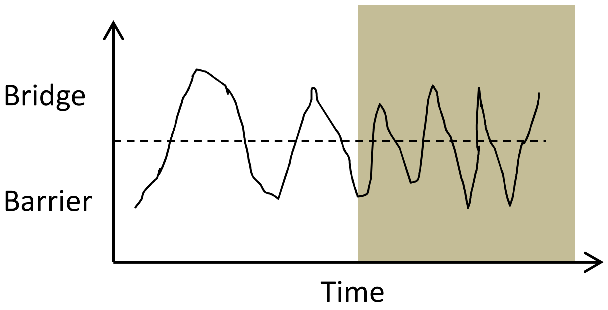
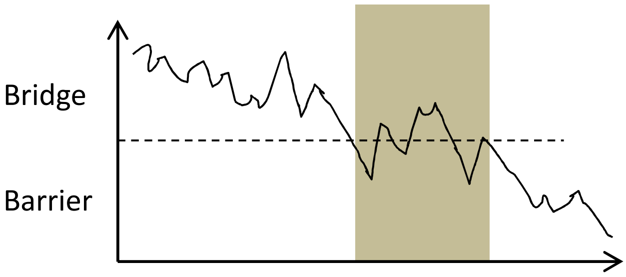
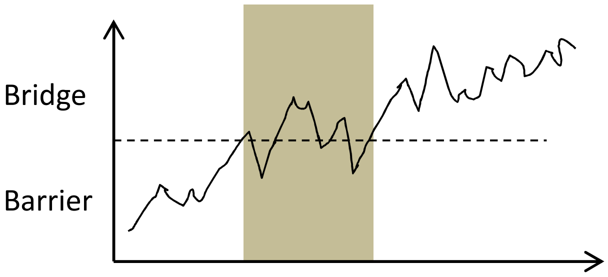
Fig. 2. Probabilities of Atlantic Bluefin tuna (ABFT) occurrence deduced from the NPPEN niche model (see Fromentin et al., 2014a): (a) for the entire period (1960 to 2009); (b) anomalies of the probabilities of ABFT occurrence during the “Brazilian episode” (computed as the map of ABFT occurrence over 1960 to 1967 minus the median probabilities calculated in each pixel from 1960 to 2009); and (c) same as (b) for the period 2000 to 2009 (from Fromentin et al., 2014a)

Fig. 3: Juvenile Atlantic Bluefin tuna potential feeding habitat (expressed as frequency of occurrence) during migration period after wintering (from April to June) in 2009 (panel a), 2010 (panel b) and 2011 (panel c). The potential habitat of juvenile Atlantic bluefin tuna is derived from the daily detection of chlorophyll-a fronts and a tolerance to sea surface temperature (see Druon et al. 2016 for more details). Blanks indicate a frequency of occurrence lower than 1%. The 200 m depth contour is shown. Panel d) shows the mean occurrence of juvenile bluefin tuna feeding habitat in the central area of the bridge, represented by a box (36-48°N, 35-57°W) in panels a, b and c, from April to June in each of the years.

Fig. 4. Habitat preferences for juvenile SBT based on sea surface temperature (°C) and chlorophyll a (mg/m3; log scale) for the area 25-45°S, 80-180°E during April-June of 1998-2000 (a; n=46 fish) and 2004-2006 (b; n=24 fish); only fish ≥ 85 cm were included for consistency between the two periods. Preferences were calculated by comparing environmental data where SBT were located with environmental data for the whole area during the time period of interest. Values >1 indicate preferred habitat (i.e. conditions at which fish are found in greater proportion than they occurred in the ocean) (see Basson et al., 2012). The maps show areas around Tasmania containing preferred SBT habitat (values >1) in April-June of 1998-2000 (c) and 2004-2006 (d), based on the habitat preference model for the corresponding time period.

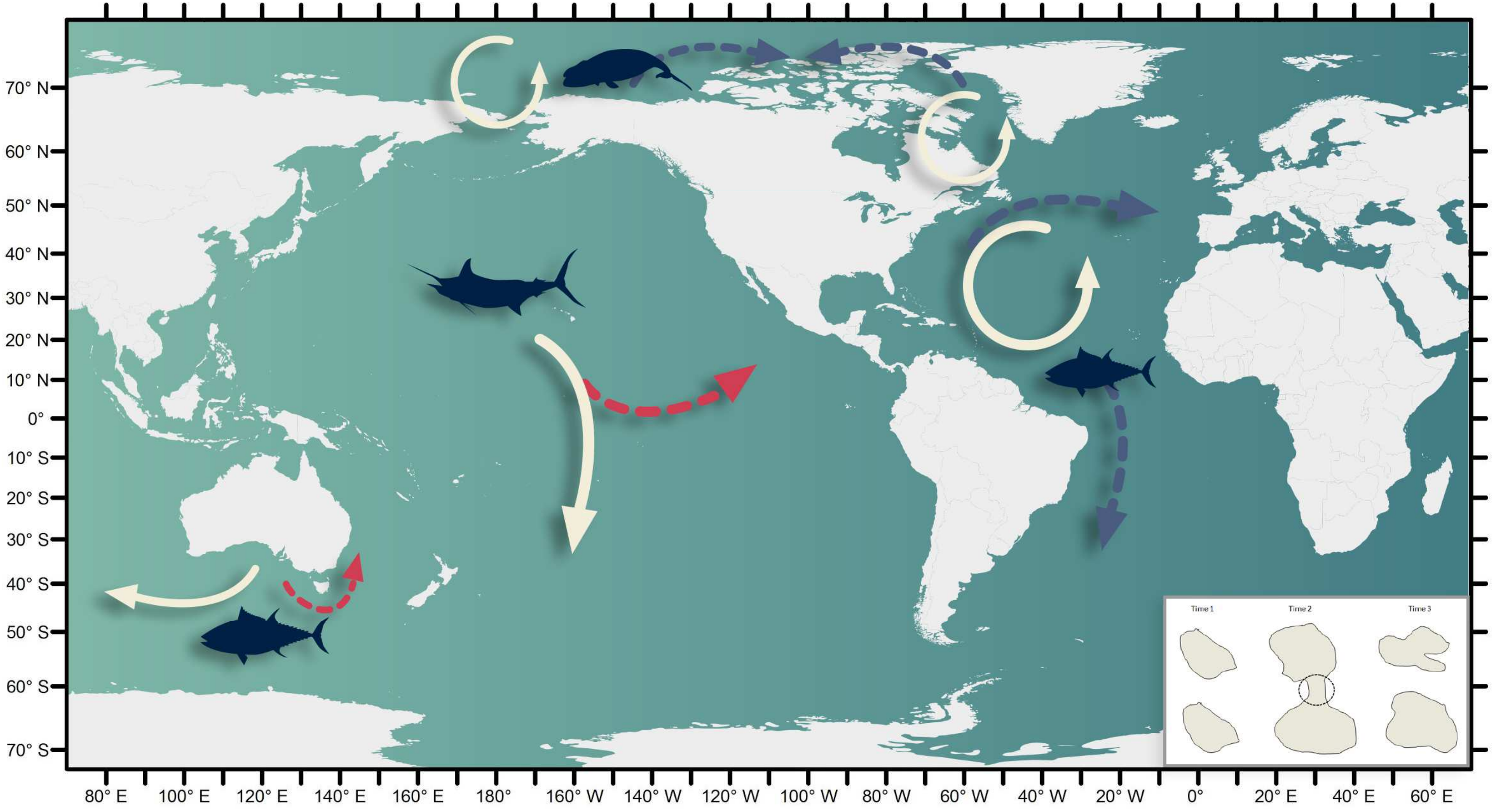
Fig. 5: Trans-equatorial movements of blue marlin during the 2009 El Nino (right) and 2010 La Nina (left). Remotely sensed sea surface temperature is from October 2009 and 2010. Tracks from 2009 and 2010 are shown, with the thick black sections showing period of track corresponding to period for remotely sensed SST data. Note that fish crossed the equator during every year of tagging except for during the 2010 La Nina (left). From Carlisle et al. (In Review).

Table 1. Schematic illustration of oceanic systems with bridge and barrier conditions over time. Shaded grey area indicates time periods when the periodicity has changed in A, and where bridges and barriers occur in B and C.

Mode	Example	Implications
A. Increasing periodicity of bridge conditions  	Blue marlin – El Nino conditions break bridge more often	Context-dependent
B. Declining frequency of bridge conditions  	NW passage in historical times Salmon shark in north Pacific[1] Swordfish in Pacific[2]	Decreased connectivity, increase in metapopulations and possible speciation
C. Increasing frequency of bridge conditions  	Bowhead whale – NW passage[3]	Increased connectivity across species range – loss of metapopulation structure

References: [1]Weng et al. (2005), [2]Reeb et al. (2000), [3](Heide-Jørgensen et al., 2012)

Fig. 1. Examples of ecological bridges and barriers for five populations of pelagic species along their migratory routes (solid white line). Dashed lines represent individual movements upon the formation of a bridge (blue) or a barrier (red). Inset: Schematic showing an ecological bridge connecting two ocean regions (time 2; dashed circle) that was not connected before (time 1) or after (time 3).



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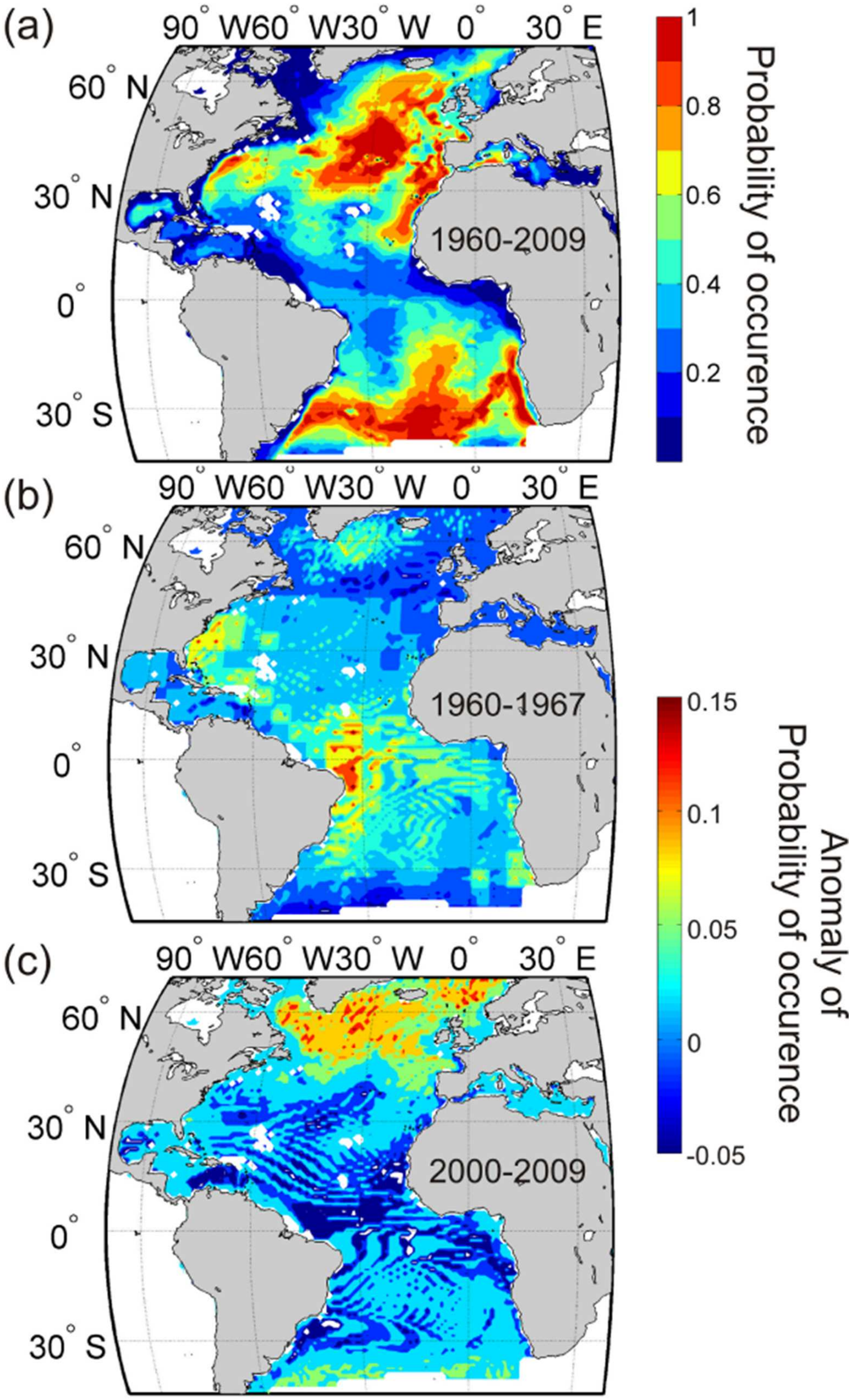

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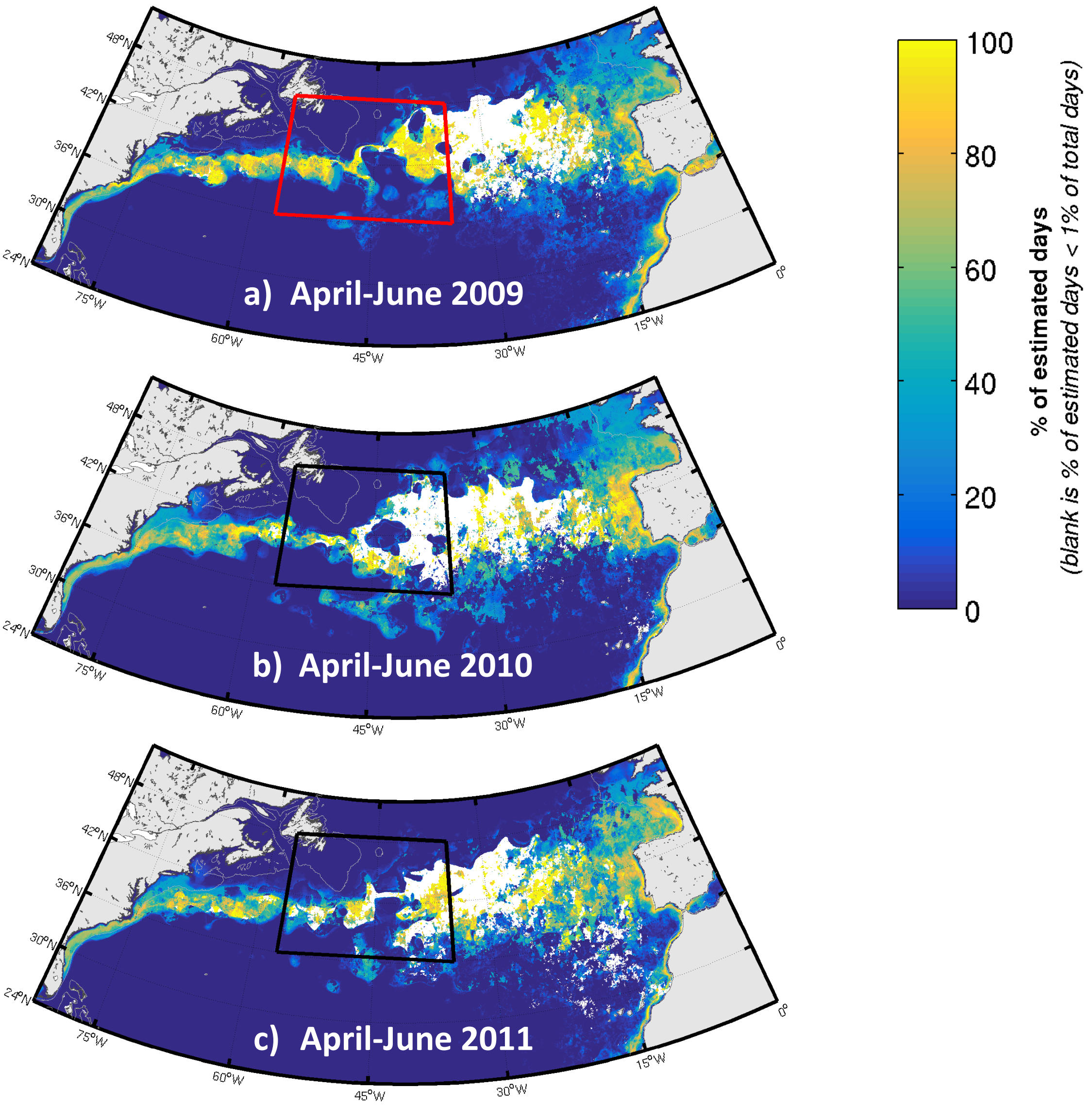
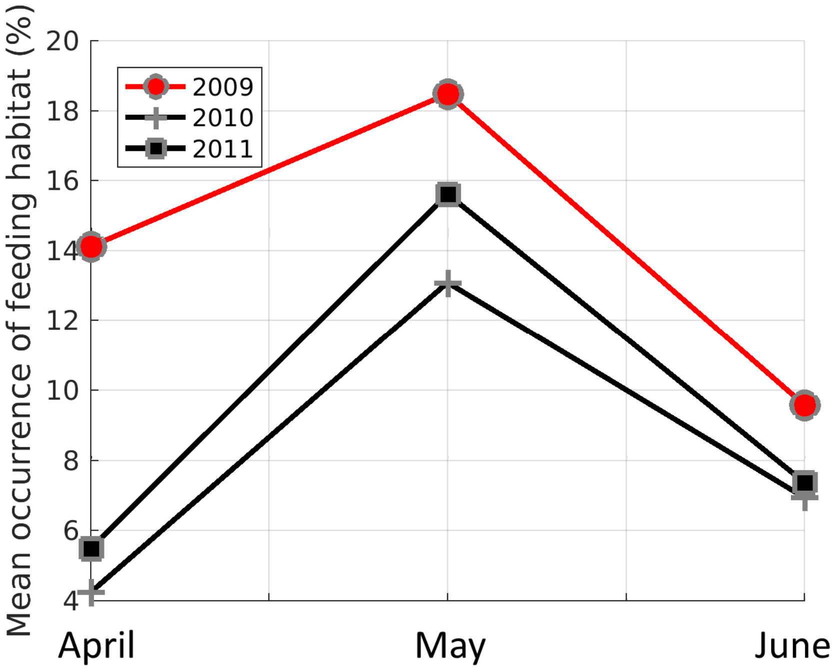


d)


Mean occurrence of feeding habitat (%)
20
18
16
14
12
10
8
6
4
2009
2010
2011
April
May
June

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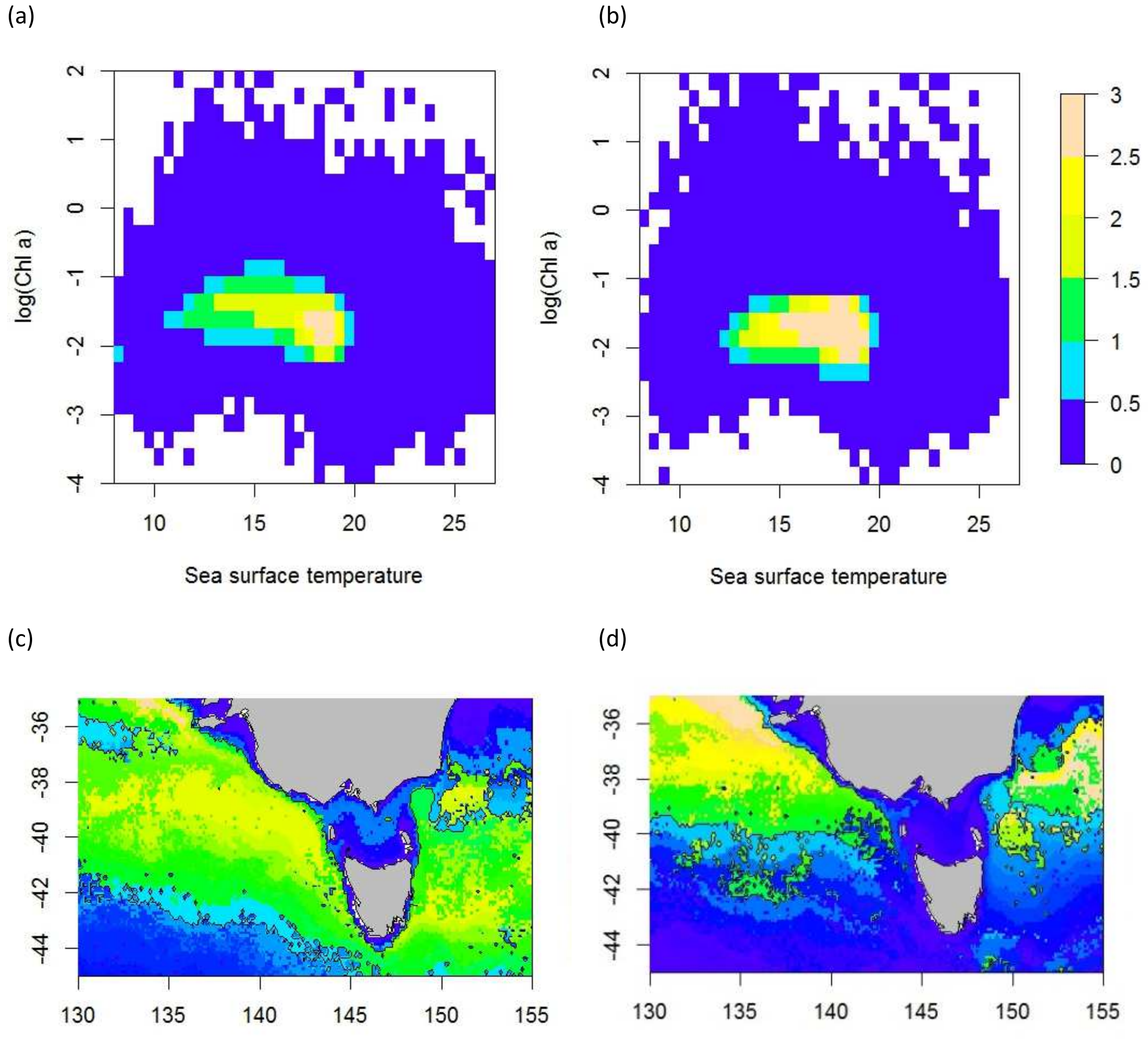

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