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Ecological dispersal barrier across the equatorial Atlantic in a migratory planktonic copepod

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ABSTRACT

Resolving the large-scale genetic structure of plankton populations is important to understanding their responses to climate change. However, few studies have reported on the presence and geographic extent of genetically distinct populations of marine zooplankton at ocean-basin scales. Using mitochondrial sequence data (mtCOI, 718 animals) from 18 sites across a basin-scale Atlantic transect (39°N–40°S), we show that populations of the dominant migratory copepod, *Pleuromamma xiphias*, are genetically subdivided across subtropical and tropical waters (global F_{ST} = 0.15, global Φ_{ST} = 0.21, both $P < 0.00001$), with a major genetic break observed in the equatorial Atlantic (between gyre F_{CT} and Φ_{CT} = 0.23, $P < 0.005$). This equatorial region of strong genetic transition coincides with an area of low abundance for the species. Transitional regions between the subtropical gyres and the equatorial province also harbor a distinct mitochondrial clade (clade 2), have higher haplotype and nucleotide diversities relative to the northern and/or southern subtropical gyres (e.g., mean h = 0.831 EQ, 0.742 North, 0.594 South, $F_{2,11}$ = 20.53, $P < 0.001$), and are genetically differentiated from the majority of sites in the central gyre and temperate zones of the same hemisphere (significant pairwise Φ_{ST} 0.038–0.267, 79% significant). Our observations support the hypothesis that regions of low abundance within species mark areas of suboptimal habitat that serve as dispersal barriers for marine plankton, and we suggest that this may be a dominant mechanism driving the large-scale genetic structure of zooplankton species. Our results also demonstrate the potential importance of the Atlantic equatorial province as a region of evolutionary novelty for the holoplankton.

1. Introduction

The genetic structure of a species plays an important role in its capacity for adaptation to environmental change by establishing the spatial scale over which populations exchange alleles (Sanford and Kelly, 2011). Resolving the large-scale genetic structure of zooplankton populations is therefore important to understanding the potential responses of these species to climate change. Few studies have reported on the presence and geographic extent of genetically distinct populations of marine zooplankton at ocean-basin scales, and little is known regarding the oceanographic and ecological processes that drive the genetic patterns observed. Many nominal zooplankton species have cosmopolitan distributions across subtropical and tropical waters worldwide (e.g., Brinton, 1962; Fleminger and Hulsemann, 1974; van der Spoel and Heyman, 1983), and while some of these are in fact cryptic species complexes (e.g., Goetze, 2010a,b; Cornils and Held, 2014; Hirai et al., 2015), others share mitochondrial haplotypes across vast ocean expanses and are true biological species distributed across several ocean basins (e.g., Goetze, 2005, 2011; Norton and Goetze, 2013). Studies of population structure in the latter, 'true' cosmopolitan species have revealed: (1) significant population structure often occurs at ocean gyre and basin scales, (2) genetic breaks are observed between the northern and southern hemisphere populations in all species examined to date, (3) spatial structuring at gyre and basin scales is often coupled with chaotic genetic patchiness at finer geographic scales (within gyres), and (4) genetic structure among populations in different ocean gyres is temporally stable in some cases (*Eucalanus hyalinus*, *E. spinifer*, *Haloptilus longicornis*, *Pleuromamma xiphias*; Goetze, 2005, 2011; Norton and Goetze, 2013; Andrews et al., 2014; Goetze

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et al., 2015). These observations, in combination with additional work documenting population structure of zooplankton species in coastal seas and estuarine habitats (Papetti et al., 2005; Peijnenburg et al., 2006; Patarnello et al., 2010; Chen and Hare, 2011), have transformed our perception of zooplankton as universally 'high gene flow' species (Peijnenburg and Goetze, 2013), and demonstrated that dispersal can be limited even in open ocean, high dispersal systems.

Identifying the drivers of genetic structure in zooplankton species is high priority but challenging, due to the limited number of studies that have been conducted at ocean basin spatial scales, and with rigorous sampling. Prior global studies on the mesopelagic copepod *Haloptilus longicornis* identified one pattern that may indicate an important mechanism driving genetic structure in zooplankton populations (Norton and Goetze, 2013; Andrews et al., 2014; Goetze et al., 2015), and testing the generality of this observation is a primary goal of this study. We hypothesize that regions of low abundance within species mark areas of suboptimal habitat that serve as strong dispersal barriers for marine plankton, resulting in the geographic co-occurrence of strong genetic breaks within species with areas of low densities of animals. Within *H. longicornis*, we observed a bimodal pattern of abundance across a basin-scale transect in the Atlantic Ocean (Atlantic Meridional Transect cruise 20 – AMT20), with high abundance in the oligotrophic gyres and low abundance in the equatorial province (Norton and Goetze, 2013; Andrews et al., 2014). This region of low animal abundance coincided with the location of a major genetic break in the species (*H. longicornis* species 1), with significant shifts in mitochondrial cytochrome *c* oxidase subunit II (mtCOII) haplotype and nuclear microsatellite allele frequencies occurring across this zone, despite the continuous distribution of the species (Norton, 2013). Given the significant genetic structure observed between subtropical gyre populations, the animals sampled within the equatorial province *cannot* represent successful migrants that are moving among gyres. Habitat discontinuities are known to serve as dispersal barriers in a variety of marine species, with population genetic structure then linked to habitat continuity across the distributional range (Johansson et al., 2008; Alberto et al., 2010; D'Aloia et al., 2014). In the case of holozooplankton, animals are continuously or seasonally transported among ocean regions with many animals advected out of their primary habitat (e.g., Tittensor et al., 2003; Speirs et al., 2006; Rullyanto et al., 2015), resulting in a biogeographic range with both source and sink populations (e.g., Miller et al., 1998; Melle et al., 2014). As a result, the presence of animals within any given ocean region may not be indicative of their capacity to sustain a viable population there. This dynamic pelagic biogeography may lead to genetic discontinuities across the distributional range, despite the continuous occurrence of the species across a variety of ocean ecosystems.

In the present study, we extend our work on population genetic structure of Atlantic zooplankton to another species, *Pleuromamma xiphias*, and examine the relationship between animal abundance and genetic discontinuities across the distributional range. Our target species, *P. xiphias*, is a cosmopolitan and mesopelagic species, but in this case with strong diel vertical migratory behavior (total length 3.25–6.42 mm; Steur, 1932; Roe, 1972; McGowan and Walker, 1979; Haury, 1988). This species migrates to the near surface to feed during darkness (upper 160 m), and returns to a resting mesopelagic depth (>400 m) during the daytime, as a predation avoidance strategy. Due to this behavior, they are important members of the migratory assemblage that mediates the active flux of carbon and nitrogen from the surface ocean to the mesopelagic zone (Steinberg et al., 2000). Prior genetic work on this species examined the population structure in primarily the Pacific and Indian Oceans, using the mitochondrial marker cytochrome *c* oxidase subunit I (mtCOI, Goetze, 2011). Sampling in the Atlantic Ocean was limited to four sites, and it was recognized that a broader survey of oceanic habitats in the Atlantic would be required to fully characterize the basin-scale structure of the species. Genetic differentiation was observed between the subtropical (MP3-09, MP3-12, 29°N) and equatorial (MP3-16, MP3-21, 11°N, 9°N) Atlantic sites, with one mitochondrial clade restricted to the two equatorial sites sampled in the western Atlantic Ocean (clade 2).

In this study, we test the generality of the link between regions of low animal abundance and dispersal barriers, by quantifying the abundance and characterizing the population structure of the cosmopolitan copepod *P. xiphias* across the Atlantic Ocean. We estimate the basin-scale patterns of abundance for this species with data from 20 sites across an oceanographic transect spanning temperate/boreal to tropical ecosystems (39°N to 40°S, Atlantic Meridional Transect cruise 22). Using mtCOI sequence data from 718 animals sampled across 18 sites, we then characterize the spatial genetic structure within the species across the same ocean transect. Our goals are to (1) characterize the basin-scale population structure of this species in the Atlantic Ocean, and (2) test for geographic co-occurrence of regions of low animal abundance with areas of major genetic transition within the species. We show, as expected, that the equatorial province serves as a major dispersal barrier for *P. xiphias*, with strong genetic differentiation of populations across this region coinciding with an area of low animal abundance.

2. Materials and methods

Bulk plankton samples were collected on Atlantic Meridional Transect Cruise 22 (AMT22) between 10/13/2012 and 11/19/2012. Oblique tows were conducted with bongo nets (200 μm, 333 μm), towed between on average 324 m depth and the sea surface. A General Oceanics flowmeter (2030RC) mounted in the mouth of the 200 μm net was used to measure seawater filtered during the tow. Seawater temperature and chlorophyll *a* concentration data in the upper 300 m of the water column were obtained using a Sea-Bird Electronics 3P Temperature Sensor and Chelsea MKIII Aquatracka Fluorometer, with data calibrated and archived by the British Oceanographic Data Centre (BODC). Plankton from the 200 μm mesh net was bulk preserved immediately in 100% ethyl alcohol, the alcohol was changed to fresh within 12–24 h of collection, and samples were stored at −20 °C. Plankton from the 333 μm mesh net was sorted live at sea, and *P. xiphias* specimens were preserved immediately in RNALater (Ambion), followed by cryopreservation in liquid nitrogen, and long-term storage at −80 °C.

Pleuromamma xiphias abundance was estimated at 20 sites along the AMT22 cruise transect (Fig. 1, Table S1), by microscopic counts of a quantitative fraction of the 200 μm net sample (1/8 – whole sample) after preservation in ethanol. These stations spanned a wider geographic range than the material used in genetic analyses, with samples ranging across the entire Atlantic distribution of the species from 42°49.52N to 43°56.16S latitude. Both adult females and adult males were counted, with identification to species by body size and the pointed process on the anterior head (Bradford-Grieve, 1999). Comparisons of abundance among ocean biomes were made using one-way ANOVA and post hoc tests with the Holm-Sidak method, following tests for normality (Shapiro-Wilk) and equal variance. Samples were grouped according to the five ocean biomes listed in Table 1.

Specimens included in the genetic analyses in this study were collected at 18 stations, located between 39°38.82N and 40°4.39S latitude (Table 1, Fig. 1). The majority of genetic analyses focused

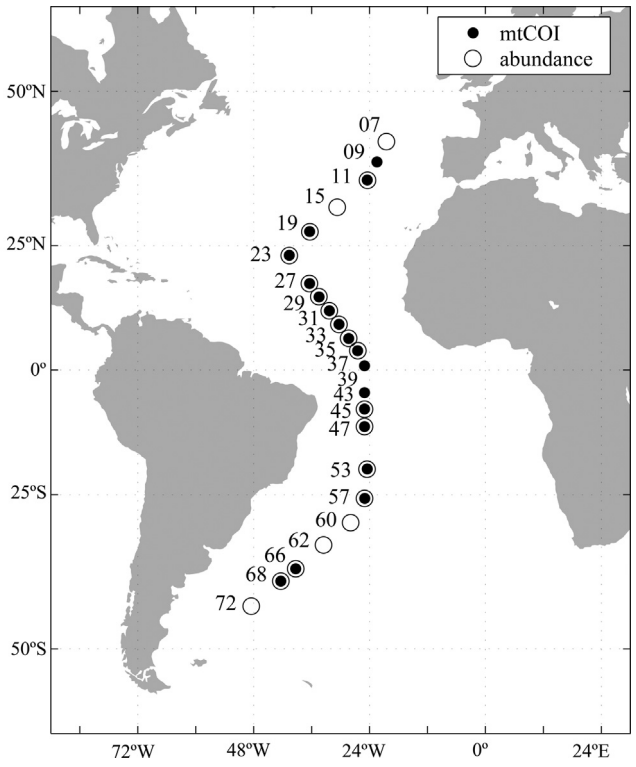

Fig. 1. Map of sampling locations included in this study, along the Atlantic Meridional Transect (AMT) cruise 22. Closed circles mark sites included in genetic analyses; open circles indicate sites used to estimate *Pleuromamma xiphias* abundance across the transect. Numbers beside each site are station numbers, as reported in Table 1.

on stations with sufficient sample size for population-level inference ($N > 42$), including AMT22-09 through AMT22-29 and AMT22-45 through AMT22-68. Specimens used in genetic analyses were primarily RNALater-preserved, but some specimens were included from ethanol-preserved samples to achieve the minimum target sample size of 45 individuals per station. When a major genetic break across the equatorial region was identified, we included samples from stations AMT22-31 through AMT22-43 to assess the genetic composition of populations across this region. Population-level analyses were not conducted on these latter stations due to small sample sizes (Table 1) and low abundance (Table S1) in this region, but sequences from these animals were included in the haplotype network reported in Fig. 3.

DNA was extracted from individual *P. xiphias* adults using the DNeasy Blood & Tissue kit (Qiagen), following the manufacturer's protocol, with the exception of longer elution incubation times (Goetze, 2011). The second of two elutions for each individual was used in this study. Polymerase Chain Reaction (PCR) amplification of a 681-bp fragment of mtCOI was conducted with primers and PCR and sequencing protocols as described in (Goetze, 2011). Forward and reverse sequences from each individual were aligned and checked for errors in Geneious (v7.1.8, Biomatters). Consensus sequences for all individuals were aligned using MUSCLE (Edgar, 2004), and unique mtCOI haplotypes were identified using FABox (http://users-birc.au.dk/biopv/php/fabox/). MtCOI sequences representing unique haplotypes are available under GenBank accession numbers KT429028–KT429159. A minimum spanning haplotype network was inferred for all mtCOI sequences using Population Analysis with Reticulate Trees (PopART; http://popart.otago.ac.nz), in order to investigate geographic patterns in the distribution of haplotypes across the Atlantic.

Population subdivision across samples was investigated using several approaches. Pairwise F_{ST} and Φ_{ST} values were calculated among all sampling sites, with significance assessed by 10,000 permutations and correction for multiple comparisons using the false discovery rate (FDR; Benjamini and Hochberg, 1995; Narum, 2006). The Akaike Information Criterion (Akaike, 1974), as implemented in jModelTest v2.1.4 (Guindon and Gascuel, 2003; Darriba et al., 2012) was used to identify the HKY + I + G nucleotide substitution model as the best fit model for our data. Pairwise and global Φ_{ST} values were calculated with the Tamura-Nei (+G) model (Tamura and Nei, 1993), which is the closest model available in ARLEQUIN (v3.5.1.3, Excoffier and Lischer, 2010). Hierarchical Analyses of Molecular Variance (AMOVA) were conducted to quantify the genetic variance partitioned between the North and South Atlantic Ocean gyres, as this was the primary division observed in the abundance data. Significance was tested with 10,000 permutations of haplotypes among populations. Haplotype (h) and nucleotide (π) diversity for each sampling site were calculated in ARLEQUIN, using the Tamura-Nei (+G) model. Comparisons of genetic diversity (h, π) among ocean regions were made using one-way ANOVA and post hoc tests with the Holm-Sidak method, following tests for

Table 1
Overview of population samples included in genetic analyses, with collection location and date, ocean biome, number of individuals sampled (N), number of haplotypes observed (H), the ratio of haplotypes to sample size (H/N), haplotype diversity (h) and nucleotide diversity (π) for each site. 'Diversity groups' indicates how samples were combined to test for differences in genetic diversity among ocean regions. 'AMOVA groups' defines the grouping of samples used in analyses of molecular variance. – Samples not included in these analyses.

ID	Cruise station	Latitude	Longitude	Date	Ocean Biome	Diversity groups	AMOVA groups	N	H	H/N	h	π
1	AMT22-09	39°38.82233N	22°27.97545W	10/16/12	North Gyre	North Gyre	North	72	20	0.28	0.7101	0.003286
2	AMT22-11	36°40.36117N	24°26.82598W	10/17/12	North Gyre	North Gyre	North	47	13	0.28	0.7234	0.002792
3	AMT22-19	27°35.97242N	36°22.42594W	10/21/12	North Gyre	North Gyre	North	124	28	0.23	0.7352	0.003055
4	AMT22-23	23°9.14204N	40°37.55777W	10/23/12	North Gyre	North Gyre	North	47	15	0.32	0.7983	0.003445
5	AMT22-27	17°42.17357N	36°27.35440W	10/25/12	Transitional N	Transitional-EQ	North	46	14	0.30	0.7739	0.004933
6	AMT22-29	15°3.37813N	34°28.44571W	10/26/12	Transitional N	Transitional-EQ	North	47	19	0.40	0.8039	0.007697
7	AMT22-31	12°13.59024N	32°23.19925W	10/27/12	Equatorial	–	–	11	9	0.82	0.9636	0.016469
8	AMT22-33	9°27.51059N	30°21.24688W	10/28/12	Equatorial	–	–	3	2	0.67	0.6667	0.016908
9	AMT22-35	6°37.12870N	28°18.99615W	10/29/12	Equatorial	–	–	6	5	0.83	0.9333	0.014372
10	AMT22-37	4°2.96024N	26°27.77399W	10/30/12	Equatorial	–	–	2	2	1.00	1.0000	0.001812
11	AMT22-39	1°7.90509N	24°59.64028W	10/31/12	Equatorial	–	–	10	7	0.70	0.8667	0.003543
12	AMT22-43	4°37.28990S	25°1.39361W	11/2/12	Equatorial	–	–	9	5	0.56	0.8056	0.014644
13	AMT22-45	8°4.63185S	25°2.39218W	11/3/12	Transitional S	Transitional-EQ	South	42	24	0.57	0.9141	0.016495
14	AMT22-47	11°36.92311S	25°2.73712W	11/4/12	Transitional S	Transitional-EQ	South	45	22	0.49	0.8323	0.011058
15	AMT22-53	20°6.17534S	24°30.99523W	11/8/12	South Gyre	South Gyre	South	70	20	0.29	0.5313	0.006619
16	AMT22-57	25°43.65371S	24°59.94407W	11/10/12	South Gyre	South Gyre	South	45	15	0.33	0.5596	0.001835
17	AMT22-66	38°4.84649S	39°18.66999W	11/16/12	South Gyre	South Gyre	South	50	15	0.30	0.6367	0.002214
18	AMT22-68	40°4.39249S	42°22.27527W	11/17/12	South Gyre	South Gyre	South	42	15	0.36	0.6469	0.003152

normality (Shapiro–Wilk) and equal variance. Samples were combined into three groups (Table 1): North Gyre, Transitional-Equatorial (both N & S), and South Gyre.

3. Results

The AMT22 transect crossed several ocean biomes, identified here as North Gyre (40°–20°N, NG), North Transitional-Equatorial (20°–12°N, NTE), Equatorial (12°N–4°S, EQ), South Transitional-Equatorial (4°–12°S, STE), and South Gyre (12°–42°S, SG) provinces (Table 1). These ocean biomes are broadly congruent with those identified in prior studies of pelagic organisms in the Atlantic Ocean (e.g., picoplankton to billfishes; Backus, 1986; Woodd-Walker, 2001; Tarran et al., 2006; Reygondeau et al., 2012), although several of these authors did not specifically distinguish the transitional regions between subtropical and equatorial provinces as we do here. Abundance of *P. xiphias* adults ranged from 7 to 178 individuals per 1000 m^3 seawater across the Atlantic transect (Table S1), between 42°49.515N and 40°4.393S. The southern edge of the species distribution was located between 40°4.393S (AMT22-68) and 43°56.161S (AMT22-72), with a complete disappearance of the species between these two stations. Abundance of *P. xiphias* was significantly different across the five ocean provinces (ANOVA, $F_{4,17} = 4.35$, $P = 0.019$), with lowest mean abundance observed in the equatorial region (mean = 34 animals 1000 m^{-3}, Table S1, Fig. 2). The equatorial province had significantly lower abundance in comparison to the North Gyre (Holm-Sidak test, $P = 0.022$), while the comparison to the South Gyre was marginally non-significant ($P < 0.06$). Station 31 was transitional and located at the northern boundary of the equatorial province, and this site had moderate *P. xiphias* abundance. Inclusion of this station in the equatorial province reduced our statistical power to detect differences between the equatorial and south gyre sites. The overall pattern of abundance was bimodal (Fig. 2), with a trend toward higher abundance at the poleward margins of the subtropical gyres and a region of low abundance within the equatorial province.

Mitochondrial COI sequence data was obtained from a total of 718 animals, with an average of 56 animals per site (range 42–124, Table 1, not including EQ sites). 145 unique haplotypes (H) were observed across all individuals (Fig. 3). Two haplotype groups were apparent in the minimum spanning haplotype network, with a 12-bp separation between them (Fig. 3). These two groups correspond to reciprocally monophyletic clades 2 and 3 from Goetze (2011). Clade 3 is cosmopolitan in subtropical waters worldwide (Goetze, 2011), and in this study, animals from clade 3 were found at all stations in the Atlantic Ocean. The two most common haplotypes in this study (H4, H1), observed in 223 and 183 individuals, respectively, were from clade 3. The majority of sampled

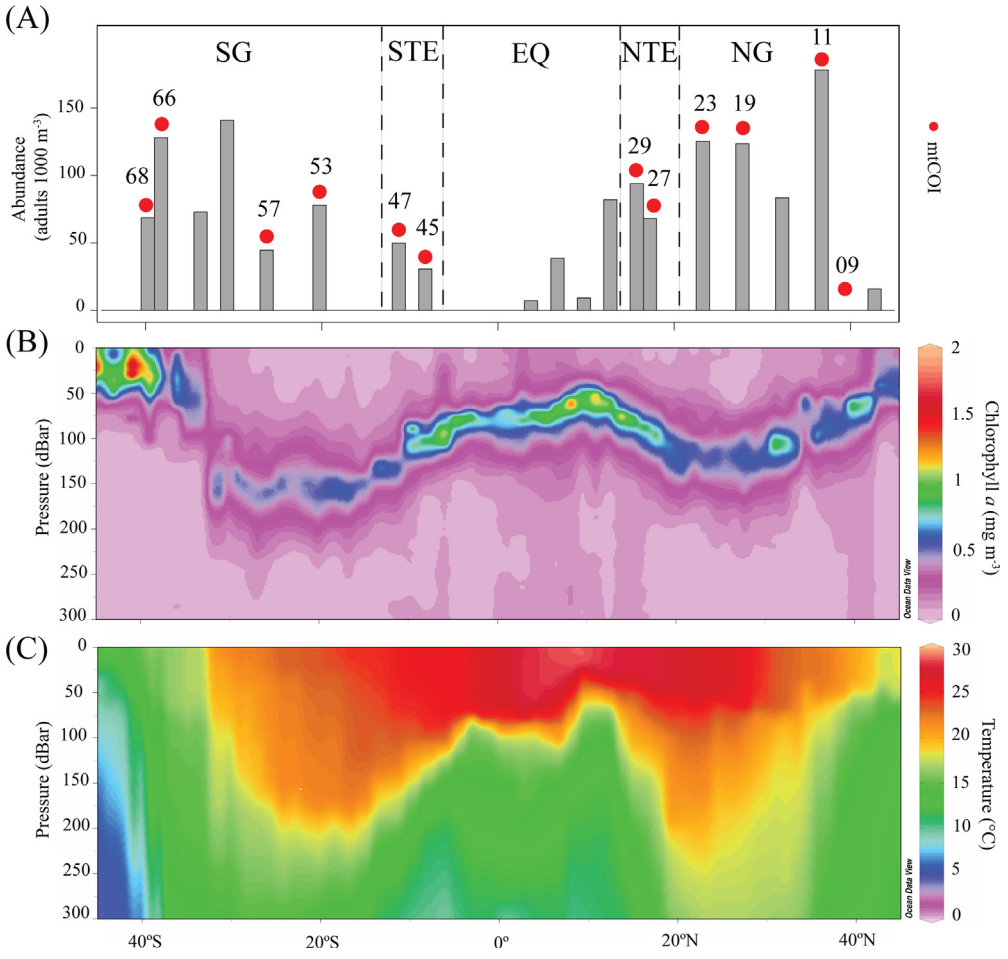

Fig. 2. Oceanographic distribution of *Pleuromamma xiphias* in the Atlantic Ocean. (A) Abundance of *P. xiphias* adults (females & males) per 1000 m^3 seawater, sampled across 20 sites on AMT22. Red circles identify stations included in population-level genetic analyses (AMT22-09 through AMT22-29, and AMT22-45 through AMT22-68, labeled mtCOI), with station numbers as listed in Fig. 1 and Table 1. The location of site 09 is shown (genetics), although no abundance data are available from this site. Provinces are labeled as follows SG = South Gyre, STE = South Transitional-Equatorial, EQ = Equatorial, NTW = North Transitional-Equatorial, NG = North Gyre. (B) and (C) Ocean section plots of chlorophyll *a* concentration (mg m^{-3}) and seawater temperature (°C), respectively, in the upper 300 m of the water column. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

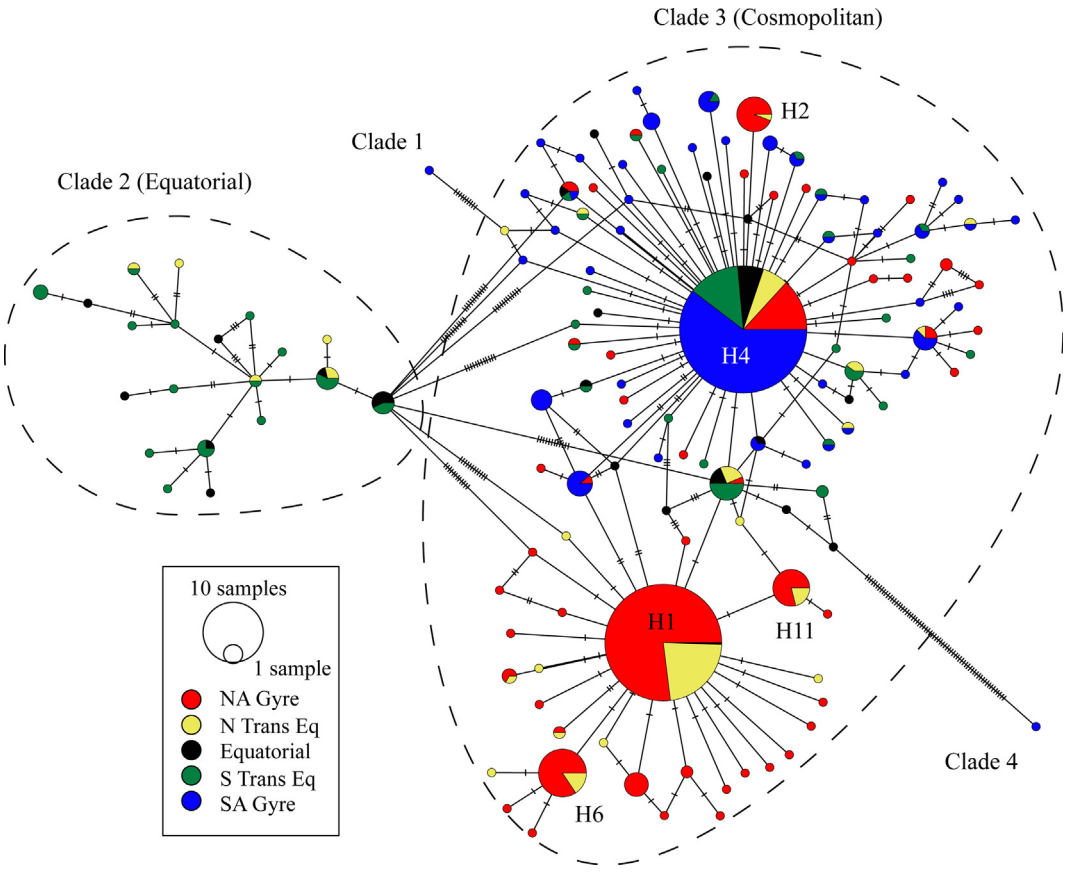

Fig. 3. Minimum spanning network of all unique cytochrome *c* oxidase subunit I (mtCOI) haplotypes sampled within *P. xiphias* in this study. Each circle represents a haplotype, with size indicative of the number of individuals sampled with that haplotype. Clade boundaries are marked by dotted lines (Clades 2, 3). Colors identify ocean provinces, with stations included as follows: 'NA Gyre' includes animals collected at stations AMT22-09, AMT22-11, AMT22-19, and AMT22-23 (North Gyre); 'N Trans Eq' includes animals from AMT22-27 and AMT22-29 (North Transitional-Equatorial), 'Equatorial' includes animals from AMT22-31, AMT22-33, AMT22-35, AMT22-37, AMT22-39, AMT22-43 (Equatorial), 'S Trans Eq' includes stations AMT22-45 and AMT22-47 (South Transitional-Equatorial), and 'SA Gyre' includes animals from AMT22-53, AMT22-57, AMT22-66, and AMT22-68 (South Gyre). Mutational steps are shown as hatch marks along each edge. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

haplotypes were only one or two substitutions away from these two common haplotypes (Fig. 3). Clade 2, with a total of 20 haplotypes, occurred only at sites between 17°42.174N and 11°36.923S, including population samples AMT22-27, AMT22-29, AMT22-45, and AMT22-47. These clade 2 haplotypes co-occurred with the more widespread clade 3 throughout the equatorial region. In addition to the clade 2 equatorial haplotypes, there were 35 haplotypes from clade 3 that also were restricted in distribution to the equatorial Atlantic and the adjacent transitional regions (between stations AMT22-27 and AMT22-47), nine of which occurred in more than a single individual (non-singletons). Finally, a single individual from each of clades 1 and 4 (Goetze, 2011) was sampled in the South Atlantic (Fig. 3), providing the first observation of these clades in the Atlantic Ocean. These clades were previously reported from the Indian and/or Pacific Oceans in Goetze (2011).

Both mean haplotype and mean nucleotide diversities were significantly different across ocean regions, in a comparison of the North Gyre, South Gyre, and Transitional-Equatorial provinces (N & S combined) (h – ANOVA, $F_{2,11} = 20.53$, $P < 0.001$; π – ANOVA, $F_{2,11} = 6.161$, $P = 0.021$). Comparisons of diversity among sites included only population samples with $N > 42$ individuals sequenced (Table 1). Holm-Sidak tests for multiple comparisons found significant differences in haplotype diversity among all three regions ($P < 0.05$), with the highest mean diversity in the Transitional-Equatorial provinces ($h = 0.831$), followed by intermediate diversity in the North Gyre ($h = 0.742$) and lowest diversity in the South Gyre ($h = 0.594$). Haplotype diversity ranged from 0.53 to 0.91 among all sites (Table 1, population samples only). For nucleotide diversity, the Transitional-Equatorial region was more diverse than both the North and South Gyres (mean $\pi = 0.01$ Trans-EQ, 0.0031 NG, 0.0035 SG, Holm-Sidak, $P < 0.05$). Nucleotide diversity ranged from 0.0018 to 0.0165 across all 12 sites (Table 1, population samples only). Approximately ¼ to over ½ of animals sampled at each site had a unique haplotype (H/N ratio, Table 1).

There was significant genetic differentiation among samples across the Atlantic Ocean, with a global F_{ST} of 0.15 ($P < 0.00001$) and global Φ_{ST} of 0.21 ($P < 0.00001$). Regional differentiation among northern and southern subtropical gyre sites was observed in several analyses, including pairwise F_{ST} and Φ_{ST} (Table 2), the minimum spanning network (Fig. 3), and hierarchical AMOVA results (Table 3). Pairwise F_{ST} values ranged from −0.010 to 0.361, with 64% significant after the false discovery rate correction for multiple comparisons (Table 2). Pairwise Φ_{ST} values were higher than pairwise F_{ST} on average, and ranged up to 0.523 (71% significant). All between-gyre pairwise comparisons were significant (range $F_{ST} = 0.101$–0.361), using either F_{ST} or Φ_{ST} as a metric (Table 2). A hierarchical AMOVA with samples grouped by subtropical gyre (north, south) also was significant ($P < 0.005$), with an F_{CT} of 0.23 among groups (F_{CT}, Φ_{CT} results identical; Table 3). This pop-

Table 2
Pairwise F_{ST} and Φ_{ST} values between all pairs of samples, with AMT22 stations as listed in Table 1 and shown in Fig. 1. Pairwise F_{ST} values are reported below the diagonal, with pairwise Φ_{ST} values above the diagonal. **Bold** values are significant following correction for multiple comparisons using the false discovery rate (FDR).

		North Atlantic						South Atlantic					
		Stn 09	Stn 11	Stn 19	Stn 23	Stn 27	Stn 29	Stn 45	Stn 47	Stn 53	Stn 57	Stn 66	Stn 68
North Atlantic	Stn 09	****	−0.004	−0.003	−0.009	0.005	**0.038**	**0.335**	**0.279**	**0.285**	**0.438**	**0.402**	**0.364**
	Stn 11	−0.009	****	0.006	0.000	0.014	**0.042**	**0.318**	**0.284**	**0.316**	**0.523**	**0.482**	**0.431**
	Stn 19	−0.001	0.006	****	−0.009	0.007	**0.045**	**0.385**	**0.313**	**0.307**	**0.430**	**0.398**	**0.369**
	Stn 23	−0.004	−0.005	−0.006	****	−0.005	0.022	**0.283**	**0.231**	**0.246**	**0.418**	**0.380**	**0.333**
	Stn 27	0.003	0.011	−0.003	−0.010	****	−0.008	**0.223**	**0.172**	**0.220**	**0.354**	**0.325**	**0.281**
	Stn 29	0.004	0.008	0.006	−0.004	−0.004	****	**0.157**	**0.112**	**0.193**	**0.277**	**0.259**	**0.222**
South Atlantic	Stn 45	**0.174**	**0.172**	**0.152**	**0.112**	**0.105**	**0.101**	****	0.016	**0.225**	**0.260**	**0.267**	**0.235**
	Stn 47	**0.206**	**0.209**	**0.178**	**0.140**	**0.126**	**0.128**	−0.001	****	**0.113**	**0.152**	**0.157**	**0.129**
	Stn 53	**0.341**	**0.361**	**0.295**	**0.280**	**0.255**	**0.277**	**0.109**	**0.064**	****	−0.003	−0.004	−0.006
	Stn 57	**0.321**	**0.338**	**0.278**	**0.257**	**0.233**	**0.253**	**0.090**	**0.050**	−0.007	****	0.006	0.002
	Stn 66	**0.288**	**0.302**	**0.250**	**0.224**	**0.202**	**0.220**	**0.065**	0.033	0.000	−0.005	****	−0.001
	Stn 68	**0.283**	**0.296**	**0.245**	**0.217**	**0.195**	**0.213**	**0.059**	0.028	0.000	−0.004	−0.005	****

Table 3
Partitioning of genetic variation among northern and southern subtropical gyre populations in *Pleuromamma xiphias*, by hierarchical analyses of molecular variance (AMOVA). Results for both F_{ST} and Φ_{ST} based analyses are reported. All fixation indices were significant at $P < 0.005$ or less. Global F_{ST} for this study was 0.15 ($P < 0.00001$), and global Φ_{ST} 0.21 ($P < 0.00001$).

Population subdivision	Metric	Source of variation	df	Variance components	% Variation	Fixation indices	
Subtropical Gyres North and South Atlantic	F_{ST}	Among groups	1	0.10613 (Va)	22.63	0.23	F_{CT}
		Among populations	10	0.00515 (Vb)	1.1	0.01	F_{SC}
		Within populations	665	0.35771 (Vc)	76.27	0.24	F_{ST}
Subtropical Gyres North and South Atlantic	Φ_{ST}	Among groups	1	0.45725 (Va)	22.78	0.23	F_{CT}
		Among populations	10	0.13501 (Vb)	6.73	0.09	F_{SC}
		Within populations	665	1.41533 (Vc)	70.5	0.30	F_{ST}

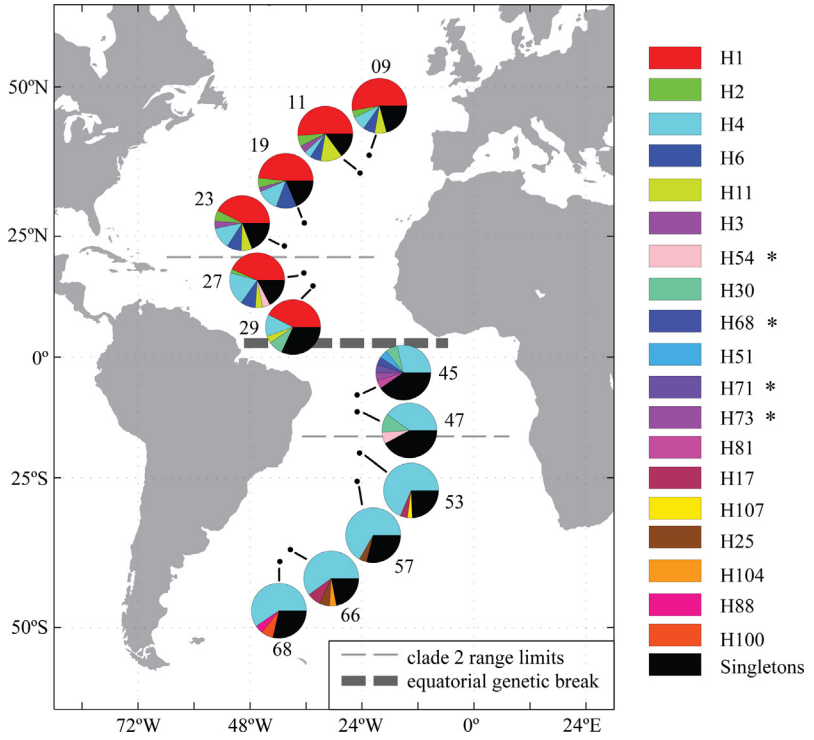

Fig. 4. Distribution of cytochrome *c* oxidase subunit I (mtCOI) haplotypes across 12 sites in the North and South Atlantic. Each pie represents a sampling site (site number shown), with mtCOI haplotypes in color as indicated by the legend (at right). The thick dashed line marks the location of a major genetic break among populations in the subtropical North and South Atlantic, and thin dashed lines indicate the northern and southern range limits for clade 2. Haplotypes with an asterisk (*) are within clade 2, in addition to some of the singletons. Only sites included in population-level analyses are shown.

ulation differentiation was driven both by the presence of private haplotypes in both the northern and southern gyres, as well as by large shifts in haplotype frequency in haplotypes that were shared among ocean regions (Fig. 4). For example, the dominant haplotype in the northern gyre, haplotype 1 (Figs. 3 and 4), was absent from all sites in the southern hemisphere. Several other less

common, but widespread haplotypes were also present only at northern gyre sites (e.g., haplotypes 2, 6, 11). The most common haplotype in the southern gyre was present in the northern gyre, but occurred in low frequency there (H4, Figs. 3 and 4). There were a few non-singleton haplotypes that occurred only at southern gyre sites, but they occurred in lower frequency than the relatively common haplotypes that were restricted in distribution to the northern gyre.

In addition to the strong and significant differentiation between gyres, we also found support for genetic differentiation between stations at the equatorward margin of each gyre in comparison to the remaining samples at the center and poleward margins of the same ocean gyre. This within-gyre pattern occurred in both the northern and southern subtropical gyres. Southern Transitional-Equatorial stations AMT22-45 and AMT22-47 were significantly differentiated from most other samples collected in the South Atlantic (pairwise F_{ST} 0.028–0.109; Table 2), with greater differentiation observed in Φ_{ST} due to the spatial distribution of clade 2 (equatorial endemics). The North Transitional-Equatorial sample AMT22-29 was significantly differentiated in pairwise Φ_{ST} comparisons (0.038–0.045) from northern gyre samples AMT22-09, AMT22-11 and AMT22-19, collected in subtropical and temperate waters. These Transitional-Equatorial stations are the same samples that contained higher haplotype and nucleotide diversities relative to the northern and southern gyres (as described above).

4. Discussion

Relatively little is known regarding the underlying population structure of cosmopolitan marine zooplankton species, due to the scarcity of studies that have been conducted at ocean basin spatial scales, over significant portions of the distributional ranges of these species. As a result, although many zooplankton species are distributed across several pelagic habitats, and may show phenotypic differences across ocean regions in morphology, reproductive ecology, phenology, or the timing and duration of diapause as well as other traits, (Bonnet et al., 2005; Durbin and Kane, 2007; Ianora et al., 2007; Johnson et al., 2008; Melle et al., 2014), it is unknown in the vast majority of cases whether this phenotypic variation is linked to underlying spatial variation in the genetic structure of the species. The underlying genetic diversity and structure of a species is critically important in the response of populations to selective pressure, and addressing this gap in knowledge is required in order to understand whether and how zooplankton species will adapt to global change (Dam, 2013; Peijnenburg and Goetze, 2013). This study addresses this gap in knowledge and makes three important contributions. First, we show that *P. xiphias* populations are highly structured genetically across equatorial waters in the Atlantic Ocean, providing further support for the inference that this province is a major dispersal barrier for Atlantic holozooplankton (e.g., Norton and Goetze, 2013; Andrews et al., 2014; Burridge et al., 2015; Hirai et al., 2015; Goetze et al., 2015). Second, we find that the location of this genetic break within *P. xiphias* coincides with a region of low abundance for the species, suggesting that geographic concordance between regions of low population abundance and genetic breaks within species may be a shared pattern across taxa within the holoplankton (e.g., Norton and Goetze, 2013). Finally, the strong and significant genetic break observed across the equatorial Atlantic occurs in parallel to a comparable genetic break across the equatorial Pacific in this species (Goetze, 2011). This observation implies that subtropical gyres represent replicated experiments in population divergence within marine holozooplankton and are particularly powerful systems for comparative studies in the evolution of pelagic animals. We discuss each of these contributions in greater detail below.

The apparent absence of strong barriers to dispersal in the pelagic environment has long shaped our thinking about the expected biogeography and population genetic structure of zooplankton species. Historically, acceptance of allopatry as the dominant geographic mode of speciation (Coyne and Orr, 2004) led to the perception that the absence of dispersal barriers presented a paradox for the origin of species in the pelagic environment (Brinton, 1957; Pierrot-Bults and Van Der Spoel, 1979), and to expectations of high dispersal, panmictic populations, and broad biogeographic ranges for planktonic species (Pierrot-Bults, 1986; Norris, 2000; Sexton and Norris, 2008). Several contemporary studies on oceanic zooplankton have documented significant genetic structure among populations (e.g., Goetze, 2005; Papadopoulos et al., 2005; Papetti et al., 2005; Peijnenburg et al., 2006; Nelson et al., 2009; Yebra et al., 2011), in contrast to early expectations for this faunal assemblage. However, few have identified the oceanographic features that function as dispersal barriers and drive the genetic patterns observed. In recent and related work on the mesopelagic copepod *Haloptilus longicornis* across comparable Atlantic basin-scale transects (AMT20, AMT22, >80° latitude), we documented one of the first major dispersal barriers in the open sea for pelagic organisms (Norton, 2013; Norton and Goetze, 2013; Andrews et al., 2014; Goetze et al., 2015). The Atlantic equatorial province functions as a biophysical dispersal barrier for *H. longicornis* species 1 (Norton, 2013), with populations in the northern and southern subtropical gyres strongly differentiated genetically, as observed in *P. xiphias* in the present study. Both *H. longicornis* s. l. and *P. xiphias* are continuously distributed across the tropics in the Atlantic; however, the strong genetic transitions observed across the equator in both species could only occur under very low (or absent) migration among populations in northern and southern subtropical gyres. Norton and Goetze (2013) suggested that the equatorial province may serve as a dispersal barrier for other species of lower epipelagic and upper mesopelagic zooplankton, based on basin-scale patterns of abundance reported for several other species (e.g., Schnack-Schiel et al., 2010). Results reported in this study provide the first confirmation that the Atlantic equatorial province has broader significance and may be a major dispersal barrier structuring populations across taxa within the holoplankton. Limited genetic data exists for pelagic nekton (Graves and McDowell, 2015), and the extent to which the Atlantic equatorial province also serves as a dispersal barrier for other wide-ranging pelagic species is unclear. Conventional tagging studies and some early genetic studies suggested that trans-equatorial migrations did not occur in several species (e.g., sailfish, white marlin, Atlantic swordfish; Ortiz et al., 2003; Graves and McDowell, 2006; Chow et al., 2007). Subsequent work has found that population stock boundaries sometimes, but do not always, coincide with the equatorial region (Atlantic swordfish, Smith et al., 2015). We expect that other studies on cosmopolitan zooplankton will find the equatorial Atlantic to be a region of genetic transition across populations within species.

A second primary contribution of this study is to illustrate the generality of the link between regions of low animal abundance and dispersal barriers for marine zooplankton. *Pleuromamma xiphias* is characterized by a bimodal pattern of abundance in the Atlantic, with a region of low abundance in equatorial waters that coincides with the location of the strongest genetic break among populations of this species in the Atlantic Ocean (Figs. 2 and 4, Table S1). This pattern replicates that observed in *H. longicornis* sp. 1 (Norton and Goetze, 2013; Andrews et al., 2014), with the exception that the *H. longicornis* sp. 1 abundance maxima are in the most oligotrophic ocean regions, while *P. xiphias* has higher abundance in the subtropical convergence zones where chloro-

phyll *a* levels are increasing in surface waters relative to the center of the gyre (Fig. 2). Given these observations, we propose a general mechanism leading to population genetic structure in marine zooplankton, whereby regions of low animal abundance mark areas of suboptimal habitat that serve as dispersal barriers, and in turn, drive large-scale spatial patterns of genetic variation within plankton species. We are not the first authors to propose this mechanism as an underlying cause of population genetic structure in marine zooplankton (e.g., Norris, 2000; Peijnenburg et al., 2006), but we are the first to provide compelling evidence that this mechanism may be driving genetic structure in oceanic species. Under this model, the primary, preferred habitats of *P. xiphias* are the subtropical convergence zones, on the poleward margins of subtropical gyres. The animals collected within the equatorial province represent expatriated animals that have been advected out of their core distributional range. Transport of a significant fraction of the population away from core population centers (e.g., up to 50%, Rullyanto et al., 2015), where they are presumably lost from the population, is common for marine zooplankton, and has been well characterized in several species (e.g., *C. finmarchicus*, *C. pacificus*, *C. marshallae*; Bryant et al., 1998; Johnson and Checkley, 2004; Johnson et al., 2006; Speirs et al., 2006; Johnson, 2007; Ji et al., 2012). There is one important observation within *P. xiphias* that is at odds with this model; That is, the presence of a mitochondrial clade that is endemic to the equatorial province and adjacent transitional waters (clade 2). Animals with clade 2 haplotypes must be resident within the equatorial region, due to the absence of these haplotypes in other areas of the distributional range. This observation raises the possibility that there may be both resident and expatriate populations co-occurring across the equatorial zone.

We know from theoretical considerations that the number of successful migrants moving among subtropical gyres must be very small to preserve the genetic differences seen between these populations (e.g., 10s of animals or less; Spieth, 1974; Slatkin, 1985, 1987; Mills and Allendorf, 1996). We therefore make the testable prediction that *P. xiphias* animals collected within the equatorial province must represent either (1) failed migrants from subtropical waters that do not successfully transit across the equatorial zone, or (2) equatorial residents that are sufficiently adapted to this ecosystem that they are selected against in the adjacent oligotrophic gyre (also failed migrants). Simulated dispersal of passive particles in ocean circulation models indicates that animals entrained in surface waters could be transported in the North Brazil Current across the western equatorial zone in the Atlantic from the southern to the northern subtropical gyre within 18 days (Norton, 2013). This period is broadly within the expected adult longevity for large-bodied, broadcast-spawning calanoid copepods (Ianora, 1998; Hirst and Kiorboe, 2002), although to our knowledge no data on longevity are available for *P. xiphias*. Given that transport of these animals among gyres should be common, failure to successfully disperse across the equatorial province implies that animals do not survive and/or do not reproduce during transit. We therefore expect that the non-resident fraction of the equatorial *P. xiphias* population should be in worse physiological condition at the time of collection, in comparison to animals collected in core population centers. Prior studies on expatriated pelagic crustaceans have documented biochemical changes that occur in animals advected outside their primary distributional range, including lower carbon, nitrogen, and lipid content, as well as increases in body water content, due to lipid and protein consumption in starving animals (e.g., Omori, 1970; Boyd and Wiebe, 1978). A number of studies have also reported altered sex ratios, reproductive output or reproductive success, and altered vertical distribution in the water column in expatriate populations relative to populations within the 'normal' range (e.g., Boyd and Wiebe, 1978; Wiebe and Boyd, 1978; Wormuth, 1985; Kobari et al., 2008; Ji et al., 2012). We expect to observe similar changes in animal condition in the non-resident *P. xiphias* animals collected within the equatorial province, in comparison to animals collected within core population centers at subtropical convergence zones. The equatorial residents of the *P. xiphias* population, in contrast, should have high fitness and high animal condition within the equatorial zone, but may be poorly adapted to the oceanographic conditions within the adjacent gyre. Further insight into how the ecological niche of a species, and the capacity of animals to survive suboptimal oceanographic conditions, controls the large-scale population genetic structure of a species will require integrated efforts that combine oceanographic, ecological and population genomic studies within single species.

A final important contribution of this study is to document parallel patterns of genetic divergence across equatorial waters of both the Atlantic and Pacific Oceans in this species (Goetze, 2011), implying that subtropical gyres represent replicated experiments in population divergence within the marine holozooplankton and could be particularly powerful systems within which to study the evolution of pelagic animals. Sampling within the Pacific Ocean reported in Goetze (2011) was sufficient to capture large shifts in mtCOI haplotype frequency and the presence of several private haplotypes between populations in the northern and southern subtropical gyres. However, sampling was not conducted along a continuous latitudinal transect, and resulted from material collected on several cruises in different years. This opportunistic sampling made it impossible to detect in the Pacific Ocean how the changing genetic composition of *P. xiphias* populations covaries with oceanographic conditions across the equatorial Pacific. Results reported in the present study for the Atlantic Ocean provide greater insight into how the ocean environment and population abundance are linked to large-scale transitions in the genetic composition of *P. xiphias* populations. Comparable patterns likely occur in the Pacific, but were spatially undersampled there. Nonetheless, the equatorial province clearly acts as a major dispersal barrier in both Atlantic and Pacific Oceans for *P. xiphias*. Transect sampling in the Atlantic also enabled us to detect symmetry across the equator in the distribution of a distinct mitochondrial clade (clade 2, Fig. 4), elevated genetic diversity in populations at the equatorward margins of the distributional range (Table 1), and genetic differentiation of transitional-equatorial sites relative to subtropical and temperate stations in both the northern and southern hemisphere (Tables 2 and 3, Fig. 4). Recent and ongoing studies of other zooplankton groups along the same AMT Atlantic Ocean transects also find novel ecotypes, morphotypes, and genotypes in the equatorial Atlantic (Andrews et al., 2014; Burridge et al., 2015, Goetze and Peijnenburg, unpub), suggesting that this may be an evolutionarily unique region for the holozooplankton.

5. Conclusions

Broadening the diversity of zooplankton species for which we have resolved the population genetic structure across significant portions of the biogeographic range is important to identifying patterns that are held in common across holoplanktonic taxa and to determining mechanisms that drive population divergence in the open sea. Results reported here, in combination with Goetze (2011), yield one of the most spatially comprehensive genetic studies for marine zooplankton to date, and provide confirmation of several patterns observed in the few earlier studies of planktonic taxa that span multiple ocean basins. In particular, this study further supports the inference that the equatorial province serves as a major dispersal barrier for a number of plankton species, and facilitates population genetic structure among northern and southern subtropical gyres. We also provide the first confirmation that

regions of low animal abundance within species coincide with the location of strong genetic breaks, suggesting that areas of suboptimal ocean habitat play an important role in generating population genetic structure within oceanic zooplankton species. The search for general drivers of population genetic structure in non-planktonic marine species has often found that there are many species-specific, site-specific, and even temporal-specific effects in comparisons across several co-distributed species (e.g., Marko, 2004; McGovern et al., 2010; Selkoe et al., 2014). Initial observations for holoplanktonic species, although far more limited than for other marine faunal groups, indicate that it may be easier to identify general patterns in plankton than for other marine taxa that vary in the extent to which larval dispersal and population structure are driven by biophysical interactions in the coastal zone (e.g., Bradbury et al., 2008; Selkoe and Toonen, 2011; Iacchei et al., 2013). Finally, our results document the underlying genetic diversity and population structure of a large-bodied and dominant member of the migratory zooplankton assemblage in subtropical and tropical waters worldwide, both characteristics of the species that will influence the response of *P. xiphias* populations to natural selection and climate change.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2016.07.001.

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