Vol. 591: 199–216, 2018
https://doi.org/10.3354/meps12521

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 19

Contribution to the Theme Section 'Jellyfish bloom research: advances and challenges'

A global estimate of genetic and geographic differentiation in macromedusae — implications for identifying the causes of jellyfish blooms

Sarah S. Abboud[1,*], Liza Gómez Daglio[1], Michael N Dawson[1,2]

[1]Quantitative and Systems Biology and [2]Environmental Systems, University of California – Merced, 5200 North Lake Road, Merced, CA 95343, USA

ABSTRACT: Jellyfish blooms are enigmatic, in part due to uncertainty surrounding the geographic extents of populations and underlying causes and effects of demographic change. We aimed to promote understanding of likely drivers of macromedusae blooms by addressing 2 questions about patterns of genetic diversity: (1) Do congeneric individuals found within the same large marine ecosystem (LME) comprise a single species? (2) Do congeneric individuals from different LMEs represent different species? We DNA-barcoded (cytochrome *c* oxidase subunit I) 804 specimens in 16 medusozoan genera across 32 LMEs. We calculated K2P pairwise sequence divergence between congeneric individuals and estimated geodesic distance between all sample locations within and between LMEs; additionally, we calculated pairwise Φ_{ST} among conspecific samples within LMEs. While LMEs reasonably served as a proxy for species in ~76% of between-LME comparisons, LME boundaries did not match species boundaries in ~24% of inter-regional comparisons. Moreover, ~19% of within-LME comparisons showed cryptic species and ~67% showed substantial intra-specific phylogeographic structure. The overall rate of mismatch of the scale of LMEs and the scale of genetic structure in macromedusae is likely >70%, because the barcoding and phylogeographic analyses employed here cannot yet distinguish even finer-scale ecologically important population structure. These results were mirrored in analyses using Longhurst's Biogeographical Provinces. Meroplanktonic species often were genetically structured on scales of 10s to 100s of km, though holoplanktonic species may be eurymictic across 1000s to 10000s of km. We also found tentative evidence of onshore–offshore, depth, and latitudinal trends in population structure. When studying the causes and consequences of jellyfish blooms, more accurate descriptions of genetic and geographic differentiation are crucial.

KEY WORDS: Biogeography · Gene flow · Global change · Hydrozoa · Latitudinal diversity gradient · Metapopulation dynamics · Scyphozoa

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Fluctuations in the abundance and biomass of large jellyfish (macromedusae) are influenced by both natural and anthropogenic environmental change as well as by life-history characteristics that vary among species and higher taxa (Dawson & Hamner 2009, Lucas & Dawson 2014). Local increases in biomass may be 'true blooms' (Graham et al. 2001, Lucas & Dawson 2014), resulting from *in situ* demographic processes affecting local recruitment, e.g. from asexual reproduction in meroplanktonic scyphozoans (Madin & Deibel 1998, Lucas & Dawson 2014, Dawson et al. 2015). Alternatively, increases may be 'apparent blooms', due to oceanographic advection aggregating ephyrae or adults at a new place (Purcell et al. 2000, Graham et al. 2001) — possibly after a 'true bloom' occurred elsewhere (Lucas & Dawson 2014).

*Corresponding author: sabboud@ucmerced.edu

© Inter-Research 2018 · www.int-res.com

Understanding the scales of these population-level dynamics is key to understanding the incidence of jellyfish blooms and the processes that cause them.

Modern blooms have primarily garnered attention due to perceived links with global climate and environmental change (Brotz et al. 2012, Condon et al. 2012, 2013, Duarte et al. 2013), regardless of whether such links are well supported or not (Gibbons & Richardson 2013, Lucas & Dawson 2014, Sanz-Martín et al. 2016). Jellyfish blooms are evident in the fossil record at least ~500 million years ago (e.g. Young & Hagadorn 2010) and can be found in relatively pristine habitats (Nagata et al. 2015), demonstrating that some blooms are natural phenomena (Arai 1997, Brodeur et al. 2008, Kogovšek et al. 2010). Yet, the occurrence of large blooms, or 'outbreaks', that exceed recent seasonal and decadal norms have been interpreted as evidence of anthropogenic forcing via environmental pH (Winans & Purcell 2010), temperature (Purcell 2005), habitat availability (Duarte et al. 2013), coastal ecosystem health (e.g. Parsons & Lalli 2002, Richardson et al. 2009), climate change (Oguz 2005), and over-fishing (Purcell et al. 1999). This has prompted a search for global patterns in jellyfish dynamics (e.g. Brotz et al. 2012, Condon et al. 2012, 2013), with studies turning to large marine ecosystems (LMEs; Sherman 1991, used in Brotz et al. 2012) and Longhurst's Biogeographical Provinces (LBPs; Longhurst 2007, used in Condon et al. 2013) as frameworks — based on abiotic conditions, habitat type, and community composition — under which to categorize data. Such global studies suggested an overall increase in gelatinous zooplankton biomass (Brotz et al. 2012) over the last 40 yr, possibly occurring in 10 or 20 yr cycles (Condon et al. 2013).

The generality of causes and responses has, however, been questioned (Condon et al. 2012). Uncertainty arises in part from data being incomplete. Reports of blooms are unevenly distributed taxonomically (Dawson & Hamner 2009, Lucas & Dawson 2014), environmental changes have been hypothesized to favor only a particular subset of medusozoans such as *Aurelia* (e.g. Parsons & Lalli 2002, Purcell 2012), many conspecific populations respond dissimilarly to the same regional drivers (Dawson et al. 2015), and there is often a dearth of relevant information (such as temperature, pH, salinity, life history, and reliable estimates of population sizes). Key analytical challenges include distinguishing the 'true' from the 'apparent' blooms and matching the scales of studies to the scales of causes and responses (Dawson et al. 2015). Matching scales has been problematic for several reasons: for example, the pelagic nature of macromedusae makes populations hard to identify, the distributions of benthic polyp populations are practically unknown, studies have had geographic and taxonomic biases, and cryptic species have led to misidentifications (Lucas & Dawson 2014). How often these combinations of factors have led to incorrect inferences about natural boundaries relevant to jellyfish dynamics is unclear, rendering general inferences about cause and effect of blooms poorly substantiated (Lucas & Dawson 2014, Dawson et al. 2015, see also Sanz-Martín et al. 2016).

Thus, it has become clear that studies of medusozoan dynamics that use local, regional, or global multi-species datasets without addressing the underlying ecological, evolutionary, geographic, or taxonomic diversity (e.g. Attrill et al. 2007, Condon et al. 2013) can be problematic (Lucas & Dawson 2014, Dawson et al. 2015). Such studies may track trends in gelatinous zooplankton but cannot parse out trends for individual populations. Identifying evolutionary lineages and their distributions is crucial for understanding the consequences of interactions between those lineages' functional traits and their changing environments (Bastian et al. 2014, Dawson et al. 2015). Different medusozoan species inhabiting the same region can display different population dynamic responses to their shared environment (Hydrozoa: Benovi et al. 1987; Scyphozoa: Brodeur et al. 2008, Bastian et al. 2014, Dawson et al. 2015). By contrast, medusozoans inhabiting different regions could display similar responses due to countergradient variation (e.g. Dawson & Martin 2001), convergence, or parallelism (Swift et al. 2016), or could display different responses entirely (Doyle et al. 2007). Understanding those patterns is important because, in turn, medusozoan dynamics can induce an array of ecological effects on primary production by phytoplankton (Pitt et al. 2009), prey dynamics (e.g. Sweetman et al. 2014), food production including commercial fish populations and aquaculture (e.g. Purcell & Arai 2001), jellyfish fisheries and tourism (e.g. Doyle et al. 2014 and references therein), and power generation (e.g. www.bloomberg.com/news/articles/2015-03-03/attack-of-jellyfish-turns-deadly-on-sea-farms-carbon-climate).

To understand patterns of population dynamics and their implications, it is imperative to understand taxonomic diversity and geographic variation. Here, we explore the geographic scales of genetic diversity in macromedusae, i.e. scyphozoans (predominantly Discomedusae) and the hydrozoan genus *Aequorea*. We aim to answer 2 questions: (1) Do congeneric individuals found within the same LME comprise a

single well-mixed species? (2) Do congeneric individuals from different LMEs represent different species? We make species-level inferences using the principles of DNA barcoding (Hebert et al. 2003) and population-level inferences using the principles of population genetics (Wright 1965) at the spatial scale of LMEs. For comparison purposes, we also present results at the spatial scale of LBPs. Subsequently, we attempt to generalize geographic scales on which macromedusae are structured genetically using geodesic distances.

MATERIALS AND METHODS

Sample and data collection

We assessed genetic diversity in 16 genera of medusozoans — *Aequorea* (Hydrozoa), *Aurelia*, *Cassiopea*, *Catostylus*, *Chrysaora, Cyanea*, *Drymonema*, *Lychnorhiza*, *Mastigias*, *Pelagia*, *Periphylla*, *Phacellophora*, *Phyllorhiza*, *Rhizostoma*, *Sanderia*, and *Stomolophus* (Scyphozoa) — from all major oceanic basins from 69.32° N to 51.84° S. We collected data in 2 ways. First, we downloaded cytochrome *c* oxidase subunit I (COI) sequences from GenBank (Table S1 in the Supplement at www.int-res.com/articles/suppl/m591p199_supp/). Second, we made new collections (Table S1) between 1995 and 2015 using a variety of sampling methods including hand-collecting at the surface, hand-drawn plankton hauls, SCUBA, and ship-based trawls. Tentacle, mesoglea, gonads, or oral arm tissue was biopsied and preserved in 70–95% ethanol and then stored at −20°C. The complete dataset, sufficient for both LME and LBP analyses, included 804 individuals from 151 unique locations (Fig. 1, Tables 1 & S1). The subset of data for LME analyses only included 606 individuals and 121 unique locations spanning 32 distinct LMEs. Some locations within LMEs were sampled for multiple genera giving a total of 135 genus-by-location combinations, i.e. 'samples' (Fig. 1, Table S1).

Whenever possible, individuals collected simultaneously at the same location were selected for analyses. When such samples were not available, specimens encompassing multiple years at the same location were combined to achieve sufficient sample sizes. When insufficient numbers of individuals were available from a single site, a centroid was chosen, and specimens within a 50 km diameter were grouped to maximize the number of sampling sites (Table S1); this approach was applied to *Cyanea* from Pechora Sea, *Lychnorhiza* from Tuapí (Nicaragua), *Phacellophora* from Lincoln City (Oregon, USA), and *Stomolophus* from Golfo de Nicoya (Cirialillo, Costa Rica).

Sample sizes varied by analysis: between-LME analyses used n = 3 per genus per location (giving 86 genus-by-location combinations), whereas within-LME analyses used n = 6 per genus per location (giving 75 genus-by-location combinations); if a genus-by-location combination appeared in both analyses, then 3 specimens were common to both. These sample sizes were chosen as a compromise between breadth and depth of sampling, and are in line with sample sizes used previously in barcoding (e.g. Ortman et al. 2010, Krug et al. 2013) and some phylogeographic inferences (e.g. Jaskuła et al. 2016, Cornils et al. 2017). In addition, we confirmed that estimates of phylogeographic differentiation using n = 6 were correlated with estimates using larger sample sizes (n = 10) for a subset of species with sufficient sequences available in GenBank (R^2 = 0.94; Supplement 2). Individuals at a particular location were selected without reference to their putative species identification to avoid biasing results toward high or low genetic diversity and to allow for consideration of sympatry.

The number of locations sampled within an LME also varied by analysis. For the within-LME analysis, we included a minimum of 2 sampling locations per genus per LME. For the between-LME analysis, each LME was represented by a single haphazardly chosen location per genus. We subsampled in this manner to (1) maximize the number of LMEs included and (2) avoid autocorrelation and an inflated sense of sample size. However, because using only 1 location per LME may decrease precision compared to using multiple locations, we conducted a preliminary analysis for the between-analysis using increased replicates for a subset of the data (Supplement 2) to assess the frequency with which a single haphazardly chosen estimate differed from the mean-of-means by more than 1 SD. Only 8 of 174 LME–LME comparisons and 17 of 160 LBP–LBP comparisons were outliers, indicating that the single sample was representative in over 89% of LME and LBP comparisons.

Final numbers of comparisons per analysis as described above are as follows: between-LME analyses included 2565 total specimen–specimen pairwise comparisons, which converts to 285 LME–LME pairs across 16 genera. Within-LME analyses included a total of 3678 specimen–specimen pairwise comparisons, which converts to 141 sample-sample pairs based on genus-specific sampling and n = 6 per sample across 12 genera.

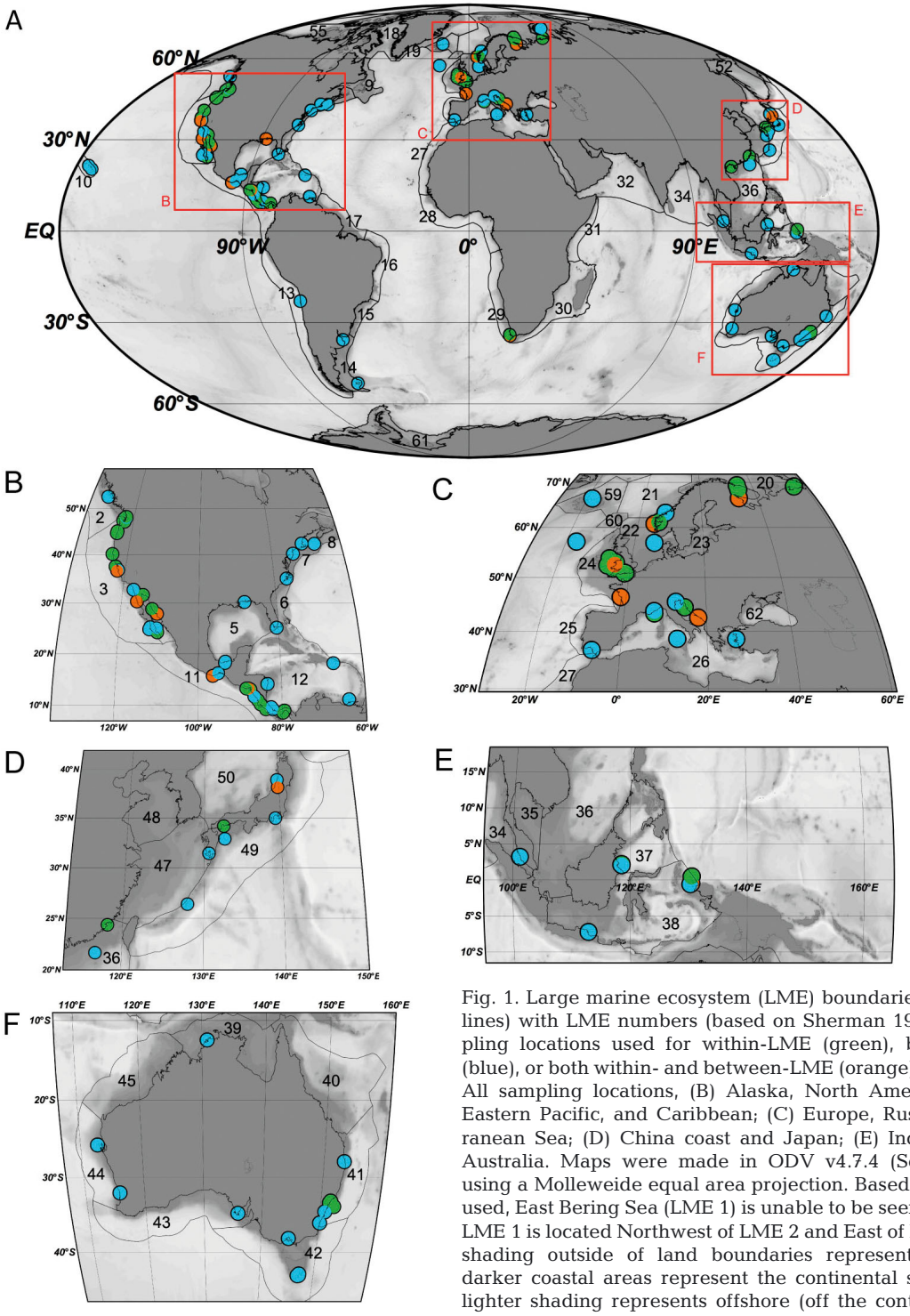

Fig. 1. Large marine ecosystem (LME) boundaries (solid black lines) with LME numbers (based on Sherman 1991) and sampling locations used for within-LME (green), between-LME (blue), or both within- and between-LME (orange) analyses. (A) All sampling locations, (B) Alaska, North America, Tropical Eastern Pacific, and Caribbean; (C) Europe, Russia, Mediterranean Sea; (D) China coast and Japan; (E) Indo-Pacific; (F) Australia. Maps were made in ODV v4.7.4 (Schlitzer 2015) using a Molleweide equal area projection. Based on projection used, East Bering Sea (LME 1) is unable to be seen on this map, LME 1 is located Northwest of LME 2 and East of LME 52. Grey shading outside of land boundaries represent bathymetry, darker coastal areas represent the continental shelf whereas lighter shading represents offshore (off the continental shelf)

DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from 381 individuals using a modified cetyltrimethylammonium bromide (CTAB) phenol-chloroform protocol (Dawson & Jacobs 2001). Previous studies have demonstrated that the COI gene sequence provides sufficient inter-specific variation to discriminate species within most medusozoans (Dawson & Jacobs 2001, Bayha & Dawson 2010). We set up 30 µl PCR reactions containing 0.6 µl of DNA template, 0.6 µl of GeneAmp dNTP Blend 10 mM (Applied Biosys-

Table 1. Number of samples per macromedusa genus in the 32 large marine ecosystems (LMEs) included in analyses. LME names and numbering convention follow Sherman (1991). Cell shading indicates when comparisons include the LME as part of the within-LME analysis (green), between-LME analysis (blue), or both analyses (orange). Numbers within shaded cells indicate the number of locations sampled, each including 6 individuals, considered part of the within-LME analysis. For the between-LME analysis, each LME is represented by a single haphazardly chosen location per genus per LME that includes 3 individuals

Larger region	LME name	LME number	*Aequorea*	*Aurelia*	*Cassiopea*	*Catostylus*	*Chrysaora*	*Cyanea*	*Drymonema*	*Lychnorhiza*	*Mastigias*	*Pelagia*	*Periphylla*	*Phacellophora*	*Phyllorhiza*	*Rhizostoma*	*Sanderia*	*Stomolophus*
Arctic Ocean	Barents Sea	20						4										
	Norwegian Sea	21																
	North Sea	22											2					
	Kara Sea	58																
	Iceland Shelf and Sea	59																
Northeast Pacific Ocean	East Bering Sea	1					4											
	Gulf of Alaska	2						2				2						
	California Current	3	4											3				
Northwest Pacific Ocean	South China Sea	36	2															
	East China Sea	47																
	Kuroshio Current	49		2														
	Sea of Japan/East Sea	50																
North Pacific Ocean	Insular Pacific-Hawaii	10																
Tropical Eastern Pacific region	Gulf of California	4	4															
	Pacific Central-America	11		2		4	3			2		2					4	
Southeast Pacific Ocean	Humboldt Current	13																
Indo-Pacific region	Sulu-Celebes Sea	37			2													
	Indonesian Sea	38		2	2													
	North Australian Shelf	39																
	East-Central Australian Shelf	41		3														
	Bay of Bengal	34																
	West-central Australian Shelf	44																
Southwest Pacific Ocean	Southeast Australian Shelf	42																
Northeast Atlantic Ocean	Celtic-Biscay Shelf	24		4												5		
	Iberian Coast	25																
	Mediterranean	26										3						
Northwest Atlantic Ocean	Northeast US continental shelf	7																
	Gulf of Mexico	5																
	Caribbean Sea	12																
Southeast Atlantic Ocean	Benguela Current	29										2						
Southern Ocean	Southwest Australian Shelf	43																
	Patagonian Shelf	14																
	By genus																	
	Total no. of LMEs in between-LME analysis		8	15	9	4	8	7	3	3	2	6	6	3	4	3	2	4
	Total no. of LMEs in within-LME analysis		3	5	2	1	2	2	0	1	0	4	1	1	0	1	0	2
	Total no. of locations in within-LME analysis		10	13	4	4	7	6	0	2	0	9	2	3	0	5	0	4

tems), 0.6 µl of BSA, 3 µl of 10× PCR buffer, 3 µl $MgCl_2$, 0.75 µl of each 20 µM primer, and 0.06 units of Amplitaq (Applied Biosystems). We amplified 452–655 nucleotides of COI using one of the primer pairs listed in Table S2 and corresponding temperature conditions (Table S3), which included multiple permutations to increase the rate of successful amplification: (1) Profile 1, primers

LCOjf (Dawson 2005a) and HCO2198 (Folmer et al. 1994) following the touch-up cycle of Dawson et al. (2015); (2) Profile 2, varied Acro* primers (Bayha & Dawson 2010, K. Bayha unpubl. data) with a touch-down cycle; and (3) Profile 3, marginally successful primer combinations following conditions described in Apakupakul et al. (1999). If these conditions did not result in sufficient amplification, we utilized genus-specific primers and conditions (Table S3).

Amplicons were direct-sequenced at the UC Berkeley DNA Sequencing Facility or Sequetech (Mountain View, CA, USA). In cases where direct sequencing did not produce readable electropherograms, we cloned the amplicon using the StrataClone PCR Cloning Kit (Stratagene, Agilent Technologies), purified the cloned DNA using the StrataPrep Plasmid Miniprep kit (Stratagene), and sequenced the plasmid using universal primers T7 and T3 (Stratagene). Contigs were assembled and checked in Sequencher v 5.3 (Gene Codes Corporation). Sequence genus identities were confirmed using BLASTn v 2.5.1 (Altschul et al. 1997). All novel published sequences were deposited in GenBank (accession numbers MF742016 to MF742396, Table S1). Previously published GenBank sequences included in our analyses (n = 423) are listed in Table S1.

Phylogeographic analyses and species estimation by barcoding

Sequences were aligned using MUSCLE v.3.8.31 (Edgar 2004) and edited using Se-Al v.2.0a11 (Rambaut 2002). For novel sequences, we checked open reading frames and amino acid translations to validate the alignment of the correct loci (free of pseudogenes). jModelTest2, PAUP* v.4.0b10 (Swofford 2002), and Arlequin v.3.1 (Excoffier & Lischer 2010) compatible files were created using a combination of Se-Al v.2.0a11 and FaBox v.1.41 (Villesen 2007). We tested for appropriate models of sequence evolution for each genus dataset using jModelTest2 on XSEDE v.2.1.6 (Darriba et al. 2012) on the CIPRES Science Gateway portal v.3.3 (Miller et al. 2010); models were selected using Bayesian information criterion and corrected Akaike information criterion (Table S4). Alignments were used to calculate pairwise sequence distances (PSD) using the genus-specific models of sequence evolution and the Kimura 2-parameter (K2P) model of substitution (which is commonly used for DNA barcoding studies; e.g. Holland et al. 2004) between individuals in PAUP*. For each genus, the genus-specific models and K2P distances were significantly correlated (Spearman's rank correlation; r-values ranged from 0.32–1 and varied by genus; median r = 0.999, $p < 0.05$; Table S4; implemented in R v.3.2.2, R Development Core Team 2015). Therefore, we used intrageneric K2P PSDs (hereafter referred to as PSDs for simplicity) for all the subsequent analyses (Table S4). We used the DNA barcoding gap at 6% sequence divergence (0.06 PSD; Gómez Daglio & Dawson 2017) to estimate species-level differences. We also assessed variation (minimum, maximum, standard deviation, mean PSD values, and mean percent of PSD values) among congeneric individuals at different locations between and within LMEs. To then assess how conspecific genetic variation is distributed within an LME, we calculated Φ_{ST} among samples that differed by <6% PSD; we used 10 000 iterations with Arlequin v.3.1. Φ_{ST} is an analogue of F_{ST} estimated using pairwise sequence distance and is likewise an estimate of population differentiation. Prior to calculating Φ_{ST}, all comparisons that yielded species-level differences were excluded to avoid conflating species-level differentiation with intra-specific population structure. Pairwise Φ_{ST} estimates greater than 0.2 are an indication of differentiation due to restricted gene flow between 2 populations (sensu Wright 1965). Frequency distributions of pairwise distances and Φ_{ST} per taxon for between- and within-LME comparisons were graphed using plot.ly v.1.0 (https://plot.ly accessed in 2015 and 2016) and Microsoft Excel 2008. Negative Φ_{ST} values were assumed to be equal to zero.

LBP-specific analyses

For comparison, we replicated all analyses using LBPs (Longhurst 2007; Tables S1 & S5), which have been used in other global analyses instead of LMEs. The LBP dataset included 771 individuals, 144 unique locations spanning 28 LBPs with 164 unique genus-by-location combinations (with 93 combinations in the within-LBP analyses and 94 in the between-LBP analyses, Fig. S1 & Table S1). Since, LBPs cover a larger proportion of the oceans compared to LMEs, we were able to include the coronate scyphozoan genera *Linuche* and *Nausithoe.* LBP names can be found in Table S5. The results of the LBP analyses, which corroborated the results of LME analyses, are available in Tables S9–S12 and Supplement 3.

Genetic distance compared to geodesic distance

We estimated great circle geodesic distances (km) between all locations with congeneric samples using the *fields* package in R v 3.1.1 (Nychka et al. 2015, R Development Core Team 2014). We removed sample redundancy between LME and LBP sample sets. If congeneric location pairs were on different sides of a landmass, we used geodesic distance estimates representing the shortest distance by sea that circumnavigated the landmass(es); each geodesic distance was checked manually. We plotted Φ_{ST} (with linear lines of best fit) and mean PSD (with linear and exponential lines of best fit) values against geodesic distances for all taxa. Functions for lines of best fit were chosen based on model assumptions, data fit, and confidence in the model from evaluating either mean residual error (from plot.ly) or linear regression model p-values using R v.3.1.1.

RESULTS

Within-LME analyses

Mean K2P PSDs calculated within genera and within LMEs (a total of 3678 specimen–specimen pairwise comparisons) yielded 141 sample–sample pairs. Mean PSD values ranged between 0 and 0.20 (mean SD = 0.039; Fig. 2A, Table S6). The majority of within-LME comparisons exhibited intra-specific variation (82.2%), while only 17.8% of the original 3678 specimen–specimen comparisons had PSDs ≥ 0.06, and similarly 25.3% of the sample–sample comparisons exhibited a mean pairwise PSD ≥ 0.06 (Table S6). Seven (58%) of the total 12 sampled genera for the within-LME analysis contained multiple species within a single LME (Fig. 2A,C, Table S6): *Aequorea*, *Aurelia*, *Cassiopea*, *Chrysaora*, *Cyanea*, *Phacel-*

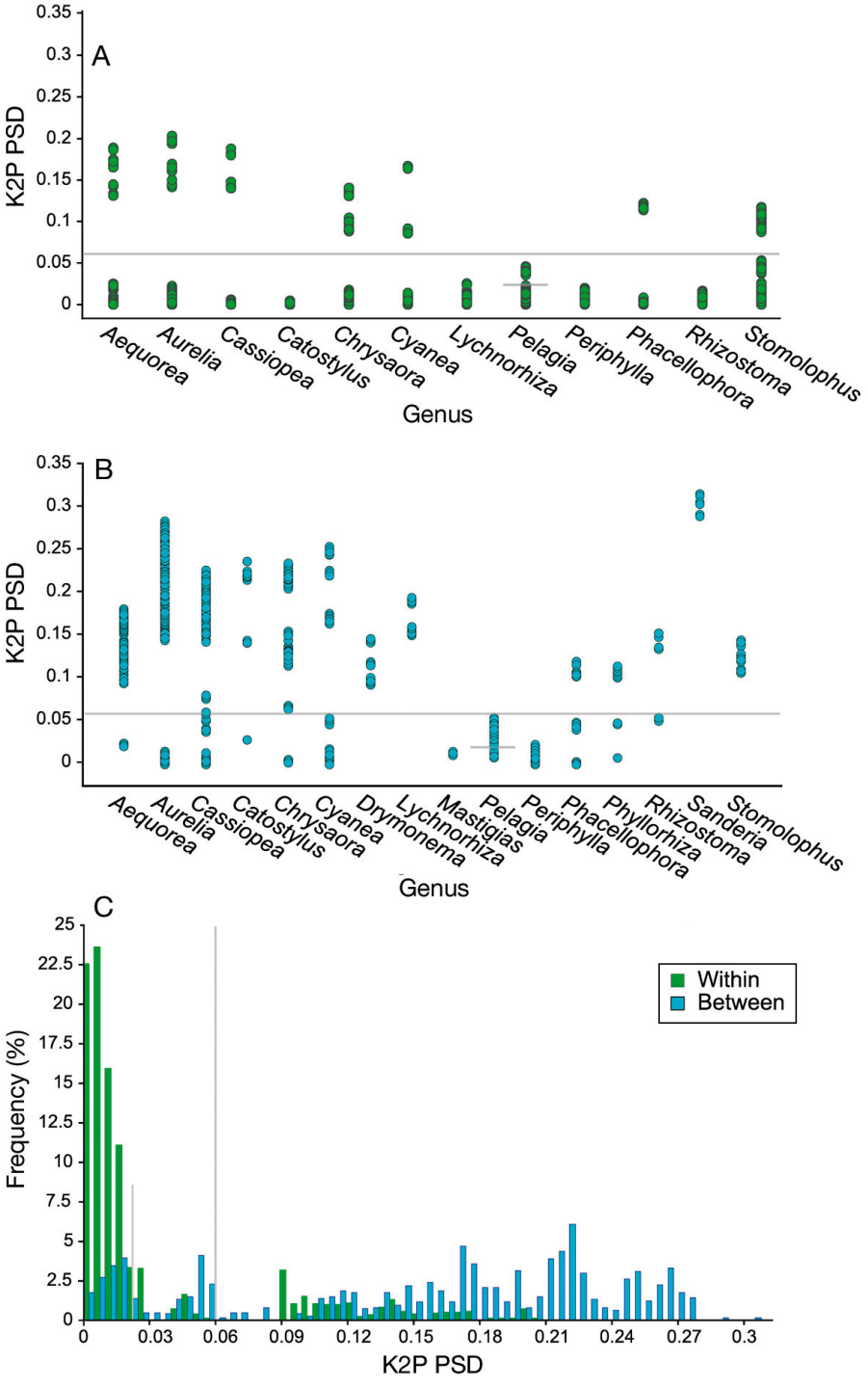

Fig. 2. Distribution of pairwise Kimura 2-parameter (K2P) pairwise sequence distances (PSD) for cytochrome *c* oxidase subunit I (COI) plotted for large marine ecosystems (LMEs) by genus for (A) within-LME comparisons and (B) between-LME comparisons. (C) Frequency distribution of COI PSD values for within- (green) and between-LME (blue) analyses. In all panels, long grey lines show PSD = 0.06 (species delimitation in this study) and short grey lines show PSD = 0.03 (possible species delimitation for *Pelagia* according to Gómez Daglio & Dawson 2017). To maximize visual ease in panel C, the *x*-axis extends only to 0.315, though a small percentage (<0.04%) of comparisons yielded PSDs > 0.315, as seen in (B)

lophora, and *Stomolophus*. By contrast, all 12 genera included at least one between-sample comparison within a single LME with PSDs < 0.06.

After excluding species-level differences from the datasets describing the aforementioned 7 genera containing multiple species within a single LME, the 56 remaining within-LME sample–sample comparisons yielded pairwise Φ_{ST} estimates ranging between −0.074 (corrected to 0) and 0.968 (SD = 0.31; Fig. 3, Tables S6–S8). Of these within-LME sample comparisons, 37.3% showed no substantive differentiation with $\Phi_{ST} < 0.05$, 13.3% exhibited $0.05 \leq \Phi_{ST} < 0.2$, and 49.4% showed significant population structure within species with $\Phi_{ST} \geq 0.2$ (Fig. 3).

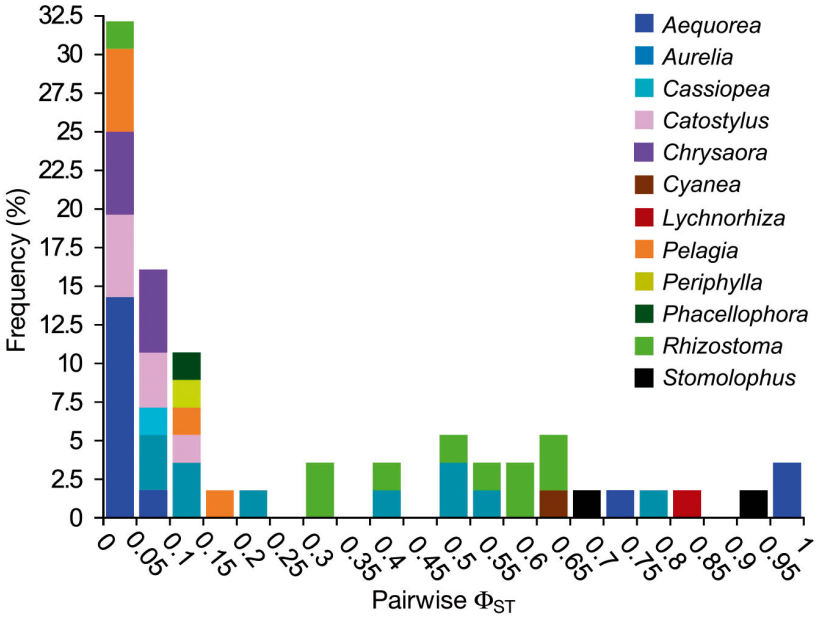

Fig. 3. Frequency distribution of pairwise Φ_{ST} values for comparisons of congeneric macromedusae within large marine ecosystems (LMEs). Percentages were all calculated relative to the entire within-LME analysis (n = 56 sample-by-sample comparisons). Genera that are absent from this figure but present in the between-LME analysis (Fig. 2B, Tables S1 & S6) were available from only one location or had sample-sample PSD values > 0.06

Considering each taxon, the highest proportion of sample–sample comparisons with $\Phi_{ST} \geq 0.2$ occurred in 3 genera: 50% of the comparisons in *Aurelia* (n_{total} = 10 comparisons), 90% of comparisons in *Rhizostoma* (n_{total} = 10), and all comparisons in *Stomolophus* (n_{total} = 2; Fig. 3). Since *Cyanea* and *Lychnorhiza* data sets only contained one sample–sample comparison, no proportions could be presented.

Considering each LME, within-LME variation differed considerably in terms of mean, median, minimum, and maximum pairwise Φ_{ST} (Fig. 4). Of the LMEs with multiple locations per genus, LMEs 3, 11, and 24 had the highest maximum genetic differentiation (Fig. 4), and LMEs 3, 11, 24, 26, and 38 had either mean or median Φ_{ST} values > 0.2, showing significant population structure within species. LMEs 20, 22, and 49 also had Φ_{ST} values > 0.2, but each dataset contained only one comparison. The remaining LMEs (1, 2, and 29) had Φ_{ST} values < 0.2 (Fig. 4, Tables S7 & S8).

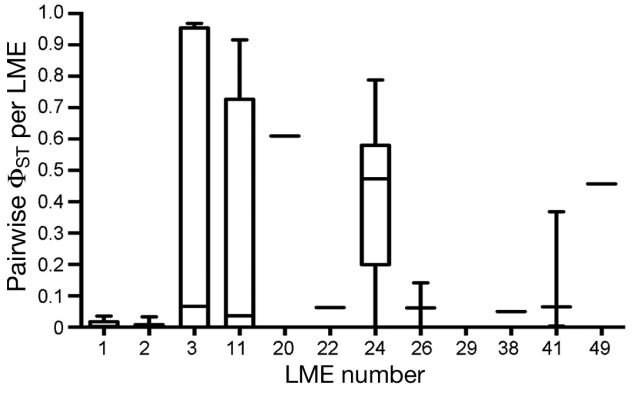

Fig. 4. Pairwise Φ_{ST} values for all taxa and location-by-location comparisons (n = 56) within each of 12 large marine ecosystems (LMEs, see Tables 1 & S1 for details) included in the within-LME analyses. LMEs are ordered by ascending LME number: East Bering Sea (1; n = 6), Gulf of Alaska (2; n = 6), California Current (3; n = 7), Pacific Central-America (11; n = 10), Barents Sea (20; n = 1), North Sea (22; n = 1), Celtic-Biscay Shelf (24; n = 16), Mediterranean (26; n = 3), Benguela Current (29; n = 1), Indonesian Sea (38; n = 1), East-Central Australian Shelf (41; n = 3), Kuroshio Current (49; n = 1). LMEs with n = 1 have the single pairwise Φ_{ST} value presented as the median. Benguela Current's (29) single sample-sample comparison yielded a Φ_{ST} value = 0. Horizontal line: median; boxes: 25th and 75th percentiles; whiskers: range

Between-LME analyses

Comparisons within genera among LMEs (n = 2565 total pairwise specimen–specimen comparisons yielded 285 LME–LME pairs) showed PSD values ranging between 0 and 0.31 (mean SD = 0.084; Fig. 2B, Table S6); of these, 24.1% had a PSD < 0.06. Twelve of the 16 sampled genera for the between-LME analysis contained a single species across 2 or more

LMEs (Fig. 2B,C): *Aequorea*, *Aurelia*, *Cassiopea*, *Catostylus*, *Chrysaora*, *Cyanea*, *Mastigias*, *Pelagia*, *Periphylla*, *Phacellophora*, *Phyllorhiza*, and *Rhizostoma*. The remaining 75.9% of all between-LME comparisons yielded PSD values ≥ 0.6, showing species-level differences (Fig. 2, Table S6). Thirteen of the 16 sampled genera exhibited different species in different LMEs: *Aequorea*, *Aurelia*, *Cassiopea*, *Catostylus*, *Chrysaora*, *Cyanea*, *Drymonema*, *Lychnorhiza*, *Phacellophora*, *Phyllorhiza*, *Rhizostoma*, *Sanderia*, and *Stomolophus*.

Genetic distance compared to geodesic distance

When plotting Φ_{ST} against geodesic distances for intra-specific comparisons only, we included n = 56 sample–sample comparisons within LMEs and n = 30 sample–sample comparisons within LBPs. Eleven genera showed significant population structure within species (i.e. $\Phi_{ST} > 0.2$) at geographic distances between ~0.9 and ~2500 km: *Aequorea*, *Aurelia*, *Cassiopea*, *Catostylus*, *Chrysaora*, *Cyanea*, *Lychnorhiza*, *Mastigias*, *Phacellophora*, *Rhizostoma*, and *Stomolophus* (Fig. 5, Tables S6–S8). The remaining taxa exhibited $\Phi_{ST} < 0.2$ for the full extent of sampling (excluding sample–sample comparisons that exhibited interspecific differences in PSDs), including *Chrysaora* (n = 6; ~170 to ~930 km), *Pelagia* (n = 5; ~50 to ~2250 km), *Periphylla* (n = 3; ~135 to ~450 km), and *Phacellophora* (n = 3; ~1020 to ~2540 km) (Fig. 5).

Excluding genus–location combinations where a centroid was used or where collections were taken at different time-points, species-level genetic distances distinguished medusae within 3 genera (*Aequorea*, *Cassiopea*, and *Cyanea*) at a geographic distance of 0 km with PSDs >0.06, i.e. congeneric species were sympatric within 1 (for *Cassiopea*) or 2 LMEs (for *Aequorea* and *Cyanea*; Fig. 6, Table S9). In within-LBP analyses, *Cassiopea* exhibited sympatry at 3 additional locations in 2 different LBPs (Fig. 6, Table S12). However, 28.9% (LME) and 22.1% (LBP) of comparisons at a given location showed only a single species per genus and that populations segregated over multiple scales: between regions, within regions, and even within a single location. *Lychnorhiza*, *Mastigias*, *Phacellophora*, and *Rhizostoma* comparisons yielded PSD values > 0.06 around ~1000 km. *Drymonema* had 1 of 3 comparisons yield a PSD value > 0.06 at a geographic distance of ~11 500 km. PSD values and geographic distances for 3 genera with only one sample–sample comparison are—*Linuche*: PSDs >0.06 at a geographic distance of ~4270 km; *Nausithoe*: PSDs >0.06 at a geographic distance of ~2650 km; and *Sanderia*: PSDs >0.06 at a geographic distance of ~11 000 km (data not shown in Fig. 6, but see Table S6). The 2 remaining taxa *Pelagia* and *Periphylla* exhibited PSD values <0.06 for the full extent of their sampling (up to ~24 500 and ~27 000 km, respectively).

DISCUSSION

Answering the key ecological genetics question about jellyfishes (and other gelatinous zooplankton)—'which species occur en masse, are on the rise (or not), where and why?' (Lucas & Dawson 2014, p. 28)—will not be simple. Multiple species may co-occur or be difficult to distinguish, yet have different bloom dynamics (Dawson et al. 2015). Many species capable of 'true' and 'apparent' blooms are composed of distinct phylogeographic lineages and likely comprise multiple metapopulations. To resolve key details and see the whole picture surrounding jellyfish blooms requires investigation of the scales of connectivity and degrees of separation among macromedusae populations.

Scales of genetic and geographic differentiation in macromedusae

So far, large-scale aggregative analyses describing global trends in jellyfish abundance or biomass (Brotz et al. 2012, Condon et al. 2013) implicitly assumed that jellyfish population dynamics occur, and are shaped by, processes acting on scales similar to those that shape LMEs or LBPs, i.e. 1000s of kilometers. The present study aimed to test that assumption and to estimate the geographic scales at which genetic differentiation actually occurs in macromedusae. We offer a first approximation of the maximum scale of population genetic subdivision in macromedusae using a global data set.

Our results show that congeneric individuals from different LMEs (or LBPs) represent different species as often as ~76% of the time; i.e. if jellyfish population dynamics occur primarily as species-level dynamics (and if our sampling is representative), then the assumption of Brotz et al. (2012) and Condon et al. (2013) is reasonable. However, jellyfish dynamics occur primarily at the population level (e.g. Dawson 2005a,b) or other similarly genetically differentiated units (e.g. Dawson & Martin 2001, Lee et al. 2013),

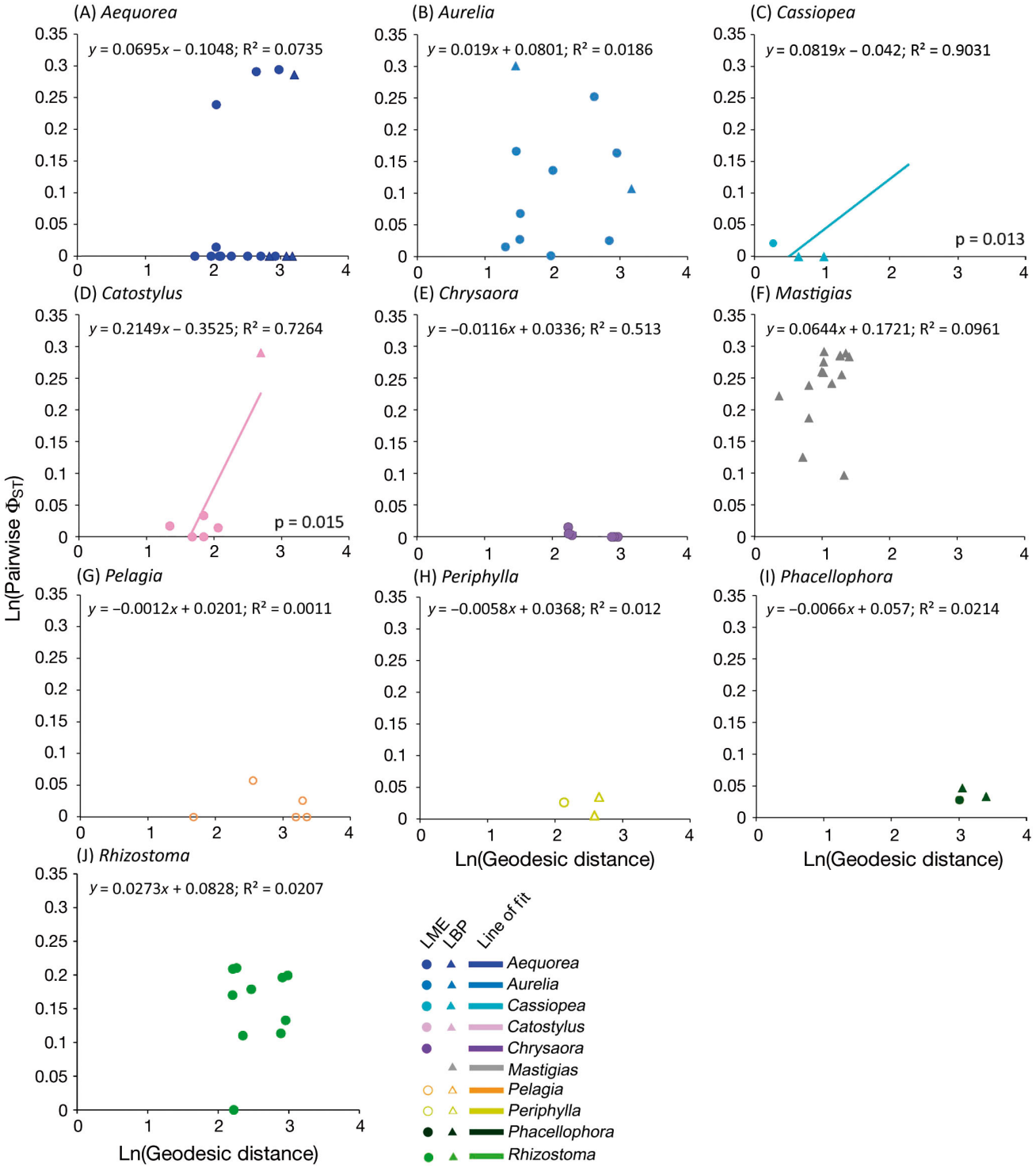

Fig. 5. Ln(Pairwise Φ_{ST}) versus ln(geodesic distance [km]) for all macromedusae included in within-analyses, i.e. including within-LME (●) and within-Longhurst Biogeographical Province (LBP; ▲) datasets. (A) *Aequorea* (n = 16), (B) *Aurelia* (n = 12), (C) *Cassiopea* (n = 5), (D) *Catostylus* (n=7), (E) *Chrysaora* (n = 6), (F) *Mastigias* (n = 15), (G) *Pelagia* (n = 5), (H) *Periphylla* (n = 3), (I) *Phacellophora* (n = 3), and (J) *Rhizostoma* (n = 10). *Cyanea* (n = 1), *Lychnorhiza* (n = 1), and *Stomolophus* (n = 2) are not presented because lines of best fit with fewer than 3 data points could not be drawn (Tables S6 & S10). Each data point represents the Φ_{ST} estimated between a pair of locations within a region (LME or LBP) where PSD < 0.06. All data points and all regions were included when plotting lines of best fit for each genus. Holoplanktonic taxa (*Pelagia* and *Periphylla*) have open symbols; meroplanktonic taxa have filled symbols. Negative Φ_{ST} values were adjusted to zero

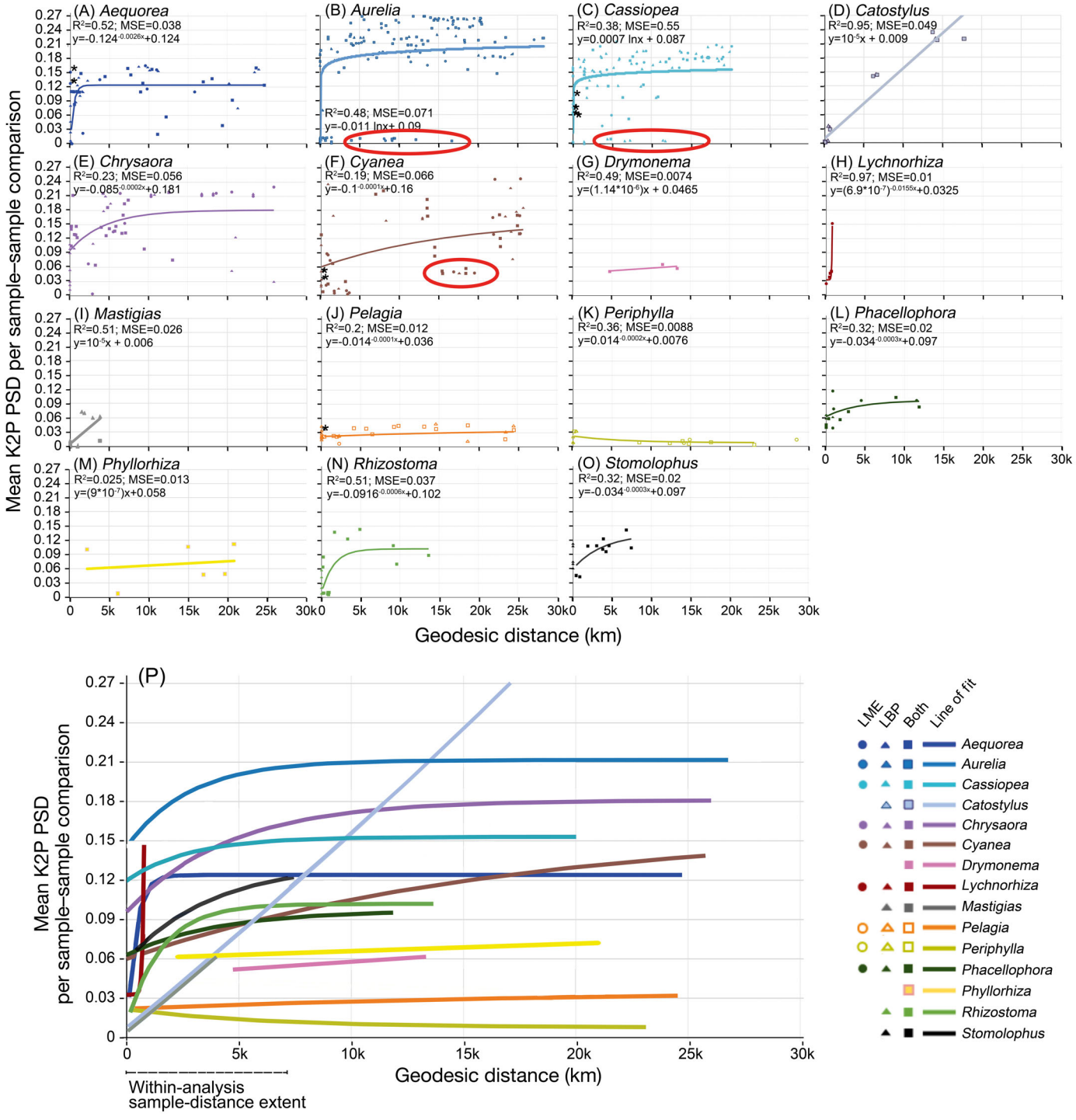

Fig. 6. (A–O) Mean K2P pairwise sequence distance (PSD) versus geodesic distance (km) for each genus. Each data point represents the mean PSD for cytochrome *c* subunit I (COI) between all individuals making up a sample–sample comparison with the line indicating the best fit. Each comparison is designated into one of the following analysis categories; LME only (●), LBP only (▲), or both (■). Open symbols: holoplanktonic taxa; filled symbols: meroplanktonic taxa. MSE: mean squared error; ⋆: instances of sympatry (excluding centroid and temporally different samples) in panels A, C, F, and J. All R^2 values were associated with p-values <0.05 except for *Drymonema* (p = 0.522) and *Phyllorhiza* (p = 0.761). Red ellipses: values that potentially indicate species introductions. (P) Lines of best fit for all genera, with dashed line below panel showing the geodesic distance range for within-analysis sample–sample comparisons

and results from asking our second research question 'whether congeneric individuals found within the same LME (or LBP) comprise a single species?' do not support the other implicit assumption of Brotz et al. (2012) and Condon et al. (2013). Our results show that congeneric individuals found within the same LME (or LBP) would be correct only ~50% of the time. Overall, if LMEs were considered the basic unit of study, there would be a ~70% mismatch of measurements at the LME scale — either underestimating or overestimating the actual scale of genetic differentiation in macromedusae (analyses at the scale of LBPs yield a similar outcome; Figs. S1–S4, Tables S1, S10–S12). In fact, 70% mismatch is likely a minimum error rate in the kinds of large-scale global analyses that have been published recently (e.g. Brotz et al. 2012, Condon et al. 2013). Barcoding and phylogeographic analyses of the kind conducted here are capable of distinguishing among well-differentiated populations and blooms resulting due to distinct lineage. However, DNA barcoding has limitations of differentiating between populations which diverged recently at which further ecological and demographic blooms may occur (Graham et al. 2001, Lucas & Dawson 2014).

Preliminary regression of Φ_{ST} on geodesic distance (Fig. 5) suggests that, as a general rule of thumb, meroplanktonic macromedusae show fine-scale population genetic differentiation ($\Phi_{ST} \approx 0.05$) over geographic distances of as little as ~3 km (e.g. *Cassiopea* from Indonesia [location codes: BMHAWSP and BMSGRDB, Table S1]), though differentiation at $\Phi_{ST} \geq$ ~0.05 becomes more common at scales of ~15–30 km in marine lake systems of Palau (e.g. in *Aurelia*, *Cassiopea*, and *Mastigias*) and ~30–300 km in coastal and more open habitats. We know of many such cases: *Aurelia aurita* in artificial lakes and adjacent sounds of southern England (15 km; Dawson et al. 2015), *Mastigias papua* in marine lakes and coves of Palau (≤20 km; Dawson & Hamner 2005), *Catostylus mosaicus* in coastal lagoons and bays of southeast Australia (60–200 km; Dawson 2005b), and *Rhizostoma octopus* in coastal bays of northwest Europe (175 km; Lee et al. 2013, Glynn et al. 2015). Scyphomedusae tend to show distinct population dynamics over these distances as well (Bastian et al. 2014, Dawson et al. 2015). More accurate estimates for oceanographic distances are still needed before rigorous statistical analyses are possible.

However, we also know of populations and dynamics that span much larger scales. *Chrysaora melanaster* in the Bering Sea appears to be genetically eurymictic on scales of 1000s of kilometers (Dawson et al. 2015). The holoplanktonic *Pelagia noctiluca* and *Periphylla periphylla* similarly appear largely genetically homogeneous on scales of 1000s to 10 000s of kilometers (Figs. 5 & 6; but see Miller et al. 2012). An outstanding question, then, is what governs the scales of population differentiation in macromedusae?

Life history, biogeographic and taxonomic correlates of differentiation

A sizeable body of literature on population genetics and observations link variation in life history traits to variation in dispersal potential, population genetic structure, and range size in many marine invertebrates and fishes (e.g. Shanks 2009, Dawson et al. 2014). To date, jellyfishes have not been included in these analyses due to a dearth of genetic data. The present study begins to fill this gap, and so we make a preliminary comparison here.

Our genetic analyses are broadly consistent with the expectation that coarse categories of life history (e.g. holoplanktonic or meroplanktonic) — paralleling the most basic informative distinctions used in fishes (e.g. Riginos et al. 2011) — may predict population genetic structure in macromedusae. The genus *Mastigias*, which is meroplanktonic, has the highest population genetic differentiation at the smallest geographic scales ($\Phi_{ST} \approx 0.33$; <5 km; Fig. 5) followed by *Aurelia* spp. ($\Phi_{ST} \approx 1$; ~27 km; Fig. 5). Multiple species of the holobenthic genus *Cassiopea* co-occurred within a single LME in approximately 80% of sampled LMEs (Figs. 2 & 6, Table S6; for LBP, see Figs. 6 & S2, Table S10). Thus, species boundaries of *Cassiopea* spp. are typically smaller than the geographic framework of LMEs or LBPs. In contrast, the holoplanktonic *Pelagia* and *Periphylla* have the least genetic differentiation of all studied genera, even across geographic distances that are orders of magnitude larger ($\Phi_{ST} \approx 0.03$; 1000s of km; Fig. 5); species boundaries of *Pelagia* and *Periphylla* thus exceed the scales of geographic boundaries separating LMEs or LBPs. At this coarse level of study, species range sizes thus also scale with life-history strategies: *Cassiopea* spp. are regional due to their benthic inhabitation, *Pelagia* and *Periphylla* are global genera due to their solely pelagic inhabitation. Population genetic structure, and likely range size, in all other species with intermediate planktonic durations (e.g. *Phacellophora*) fall between these extremes (Fig. 6), suggesting an important role for the sessile benthic polyp stage and its asexual reproduction in promoting local

population persistence and higher genetic structure in meroplankton.

The difference in Φ_{ST} between *Pelagia* and *Periphylla* over large geographic scales also suggests an oceanographic or environmental effect on population genetic structure within species. The difference — less structure in the deeper, mesopelagic *Periphylla* than in the shallower, epipelagic *Pelagia* — is consistent with patterns in other invertebrate marine taxa, which also show increasing gene flow with increasing depth (e.g. Costantini et al. 2011). Likewise, there may be an onshore–offshore pattern consistent with the idea that environmental heterogeneity may enhance biological diversity (Kostylev et al. 2005, Brodeur et al. 2008). High-dispersal holoplankton tend to be oceanic, lower-dispersal meroplankton tend to be coastal, and the low-dispersal, almost holobenthic *Cassiopea* spp. occupy perhaps the most highly structured marginal marine habitats.

Intriguingly, comparisons among geographic regions are suggestive of a latitudinal trend in diversity and differentiation. Of the 5 LMEs with the highest mean Φ_{ST} values — California Current (LME 3), Tropical Eastern Pacific Central-America (LME 11), Barents Sea (LME 20), Celtic-Biscay Shelf (LME 24), and Kuroshio Current (LME 49) — one is polar, one is tropical, and 3 are temperate. Though if we take into account PSDs by LME, we find an increasing mean PSD with decreasing latitude, resulting in increased instances of interspecific variation (Table S6). The pattern of increasing population differentiation with decreasing latitude is clearer in the dataset based on LBPs, in which the 3 provinces with both the highest median and highest overall Φ_{ST} values are tropical or subtropical (West Pacific Warm Pool Province, Sunda-Arafura Shelves Province, and East Australian Coastal), and a 4th province spanning both tropical and subtropical ranges (Central American Coastal Province) is among the 8 provinces with the highest overall Φ_{ST} values (Fig. S4, Tables S10 & S11). These trends of increased interspecific variation with decreased latitude are consistent with latitudinal gradients of genetic differentiation shown in other marine invertebrates (Kelly & Eernisse 2007) and predominant patterns of marine species diversity (Valentine & Jablonski 2015), though these supporting data are not robust evidence to make a definite claim that macromedusae show these trends, but do justify future study.

Unraveling the drivers of depth-related, onshore–offshore, latitudinal, and regional patterns of diversity in macromedusae will require considerable work. Much more information is needed on life history, habitat preferences, diet, geographical range, and other functional attributes of known species. Thorough studies of under-explored regions are needed to discover unknown species or clarify known distributions; for example, previously unknown species have been shown to be numerous, and distributions of previously known species have been expanded with exploration of the under-explored tropical Eastern Pacific Ocean (e.g. Gómez Daglio & Dawson 2017). As knowledge of species diversity increases, it will be possible to describe phylogeographic trends in biodiversity more holistically (e.g. Bowen et al. 2016) and to study its consequences statistically in global meta-analyses. Moreover, this information will help to elucidate whether these biogeographical patterns are driven environmentally, regionally, taxonomically, or functionally and, in turn, will help clarify whether intrinsic and extrinsic drivers of macromedusae population structure are related to the frequency and distribution of blooms. Preliminarily, these questions may best be explored using detailed analyses of a subset of widely co-distributed genera (e.g. *Aequorea* and *Aurelia*), which each can be compared across a wide diversity of regions.

Introduced jellyfish species

Introduced, or non-indigenous, species are a special case among taxa with wide geographic distributions. For the present study, introduced species present a challenge, because populations incorrectly identified as native (or incorrectly identified as introduced) would compromise not only inferences about natural patterns of diversity in medusae but subsequent inferences about processes influencing jellyfish blooms as well. However, the presence of introduced species is also widely acknowledged as an opportunity to study community and evolutionary ecology (Sax et al. 2007), which for jellyfishes includes local adaptation and bloom dynamics. Indeed, introduced jellyfish species may possess a particular suite of traits that enhance 'invasiveness' and predispose them to exert significant ecological and economic impacts, e.g. in the form of a bloom (Bayha & Graham 2014). Scyphozoans constitute the majority of confirmed non-indigenous jellyfish species globally and present some of the best-known case studies of jellyfish blooms (Bayha & Graham 2014). Our analyses reveal previously recognized and unrecognized species introductions, i.e. peculiar outliers in correlations of geodesic and genetic distance in Fig. 6 (based on putative species identifications only):

Aurelia sp. 1 spanning the Pacific Ocean (see also Dawson et al. 2005; Fig. 6B), *Cassiopea andromeda* being newly described in Mo'orea (see also Holland et al. 2004, Gómez Daglio & Dawson 2017 for additional introductions; Fig. 6C), *Cyanea capillata* having a newly described population in Puget Sound (see Reum et al. 2010 for previous description; Fig. 6F), and *Phyllorhiza punctata* being newly documented in Lagunda Joyuda and Bahía Magdalena (see also Bayha & Graham 2014, Gómez Daglio & Dawson 2017; Fig. 6); the correlations of geodesic and genetic distance for *Phyllorhiza*, particularly, deviates radically from geographic trends predicted from life history (Fig. 6C). These genera are all well-known invaders (Bayha & Graham 2014) and suggest that coastal meroplankton with high levels of native population differentiation may be prone to being invaders.

Implications for identifying the causes of jellyfish blooms

Analyses relying on fixed areas, such as LMEs, or a fixed geographic scale (e.g. a 5° grid; Lucas et al. 2014) are pragmatic but will often be mismatched to the actual scales and natural boundaries of jellyfish population structure. As a result, such analyses will often be mismatched to the actual scales, drivers, and consequences of jellyfish blooms.

The mismatch of fixed (large) scales of analyses to variable scales of population processes does not mean that large-scale analyses cannot yield correlations between drivers and blooms; instead, it means that large-scale analyses have yet to reliably discern the fine-scale operation of drivers responsible for blooms (Hallett et al. 2004, Paine 2010). In turn, analyses at scales smaller than populations can yield correlations between fine-scale drivers and blooms, but they can capture only a portion of the effect of processes or outcomes operating at larger scales (Brown 1999, Lawton 2000, Ricklefs 2008). Unfortunately, we have little understanding of the degree and frequency of the mismatch and its consequences for the interpretation of results. Our analyses in the present study indicate that the uncertainty surrounding the scales of processes influencing the dynamics of jellyfish blooms could be substantial and could vary by taxon, place, and time. The key challenge is to better integrate the multiple scales of jellyfish population dynamics analytically with the multiple scales of putative causes.

Meta-analyses of modular studies that are replicated globally may be an effective approach to reconcile the scales of analyses and the scales of the phenomena being analyzed (Dawson et al. 2015). This 'comparative-experimental approach … repeating similar [measurements] at large geographic scales in comparable [or contrasting] ecosystems' (Paine 2010, p. 389) is a foundation of influential studies in marine (e.g. Menge et al. 1999) and terrestrial ecosystems (Marske et al. 2013, see also e.g. Riddle 2016). The meta-analytical comparative-experimental approach may have additional benefits for studying jellyfish blooms, because widely distributed repeated measures would be more likely to sample sporadic events of variable duration, i.e. blooms, than would occasional measurements over a limited geographic range. Many blooms will likely occur in remote or poorly studied parts of the world, which justifies more thorough and representative sampling than currently occurs. Additionally, by using standardized and simple methods for specimen and data collection and analysis (e.g. plankton tows, jellyfish counts, size–frequency distributions, diameter–mass relationships, determination of reproductive status and gonadal index, nutrient analyses, and measurements of salinity, temperature, and productivity), a micro-to-macroecological meta-analysis much greater than the sum of the parts can be performed. Coordinated experimental networks, conducting sustained observational time series, will be needed to generate data for large global comparative meta-analyses on multiple spatial and temporal scales consistent with variation in the scales of jellyfish blooms and their causes. The tools for archiving such datasets are already available in part, such as the Jellyfish Database Initiative (e.g. Condon et al. 2012, Lucas et al. 2014).

Future directions

While this study is the most geographically and taxonomically comprehensive genetic analysis of macromedusae to date, it may be tempting to extrapolate this study's results to infer a global biogeography, which is commonplace for fishes, gastropods, and a few other well-known taxa (e.g. Reygondeau et al. 2012). Unfortunately, much of the ocean and many present macromedusae taxa are not yet well represented (Fig. 1). Recent surveys indicate that macromedusae are massively under-sampled (e.g. Gómez Daglio & Dawson 2017), sampled with regional biases (e.g. Condon et al. 2012, 2013), and that cryptic species are rife (e.g. Dawson & Jacobs 2001, Dawson

2005a). Resolving these shortfalls will be essential for understanding genetic and geographic differentiation of macromedusae. While COI barcoding and phylogeographic analyses have dramatically altered our perspective on scyphozoan diversity and distributions in the past 2 decades, explaining fine-scale and macroecological patterns will require information beyond such coarse estimates of species and allelic diversity.

To better estimate population structure relevant to the scales of blooms, genomic approaches will be required to identify population-level units that match the ecological scales of blooming and potential underlying adaptations. As capacity increases for 'high throughput' genomics, environmental measurements, and laboratory analyses, we also will need to increase capacity to conduct *in situ* specimen-based ecological research.

Integrating species- and population-level inferences from molecular analyses, data on morphometrics (including functional traits), and inferences from organismal and population ecology along with global data on abundances (e.g. in the Jellyfish Database Initiative) could generate an accurate and powerful tool. Mapping the resulting multifaceted patterns could help resolve which approach to marine regionalization — LMEs, LBPs, Marine Ecoregions of the World (Spalding et al. 2007), Marine Ecosystems, High Seas Areas, or fixed-degree grids (e.g. a 5° grid; Lucas et al. 2014) — best fits macromedusae or could justify creating entirely new maps specific to particular macromedusae life histories. We explored only LME and LBP datasets, with both yielding >70% mismatch between intrageneric genetic comparisons among and within LMEs and LBPs, which indicates that other approaches to evaluating regionalization will be needed. In the near term, exploration of better or more accessible maps of 'isolation by oceanographic distance' (similar to isolation by distance, commonly referred to as IBD) and 'environmental resistance' (environmental factors that inhibit migration) could help resolve boundaries established by limited dispersal versus those established by selection. In the medium term, however, static schemas will need to give way to dynamic oceanographic representations (e.g. Reygondeau et al. 2013) that accurately represent physical and biological connectivity on ecological and microevolutionary timescales.

Many ecological data on macromedusae have been collected over the past century. However, to leverage their full value via emerging databases, it is essential that field measurements be re-interpreted in light of genetic analyses and accurate species identifications, functional trait variation, environmental variation, and phylogeny. Studies that are geographically and taxonomically representative will support analyses on multiple spatial and temporal scales consistent with the ecological and evolutionary scales of jellyfish blooms.

Acknowledgements. We would like to thank N. Abboud, G. Aglieri, O. Angulo Campillo, K. Bayha, U. Bamstedt, M.E. de Bellard, T. Bolton, CEFAS crew members (M. Lilley and A. Martins), CRRF (E. Basilius, L. Bell, and P. Colin), L. Cadena Cárdenas, M. López Castro, N. Chernova, E. Cruz, D. DeMaria, V. Diaz, F. Felix, B. Hoeksema, J. Keister, D. Lindsay, C. Lucas, L. Luna Leiva, L.E. Martin, M. Martinussen, C. Meyer, H. Mianzan, B. Moreno-Dávila, Monterey Bay Aquarium, Monterey Bay Aquarium Research Institute, NOAA members (R. Brodeur, C. Greene, J. Hall, J. Harding, S. Hayes, B. Lehman, S. McIntyre, and C. Rice), W. Patry, K. Pitt, P. Strelkov, and J. Vo for contributing samples used specifically in this study (see Table S1 for all collectors who contributed to past studies that also benefitted this study). We thank S. Hayes, J. Harding, C. Rice, C. Greene, and J. Hall (NOAA), as well as A. Martins (CEFAS) for boat time. We thank those that contributed to the molecular work (no notation), provided comments that improved earlier versions of the manuscript (`), or both (*) including G. Aglieri, K. Bayha, J.M. Beman`, K. Chauhan, J. Edwards, E. Green`, M. Parekh*, M. Rocha de Souza`, A. Rosso*, S. Rutsaert, L. Schiebelhut*, J. Sexton`, H. Swift*, G. Verhaegen, J. Wilson`, J. Yeager`, and 3 anonymous reviewers. Funding for this research came from the University of California, Merced (UCM) Graduate Research Council Fellowship and Quantitative and Systems Biology (QSB) Summer Fellowships awarded to S.S.A., a National Science Foundation REVSYS award DEB-07-17071 awarded to M.ND., 2 separate Systematic Research Funds (Systematics Association and the Linnean Society of London) awarded to L.G.D., and UCM QSB research and travel grants awarded to S.S.A. and L.G.D. for discrete subsets of the project.

LITERATURE CITED

Altschul SF, Madden TL, Schaffer AA, Zhang J, Zhang Z, Miller W, Lipman DJ (1997) Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. Nucleic Acids Res 25:3389–3402

Apakupakul K, Siddall ME, Burreson EM (1999) Higher level relationships of leeches (Annelida: Clitellata: Euhirudinea) based on morphology and gene sequences. Mol Phylogenet Evol 12:350–359

Arai MN (1997) A functional biology of Scyphozoa. Chapman & Hall, London

Attrill MJ, Wright J, Edwards M (2007) Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. Limnol Oceanogr 52: 480–485

Bastian T, Lilley MK, Beggs SE, Hays GC, Doyle TK (2014) Ecosystem relevance of variable jellyfish biomass in the Irish Sea between years, regions and water types. Estuar Coast Shelf Sci 149:302–312

Bayha KM, Dawson MN (2010) New family of allomorphic jellyfishes, Drymonematidae (Scyphozoa, Discomedu-

sae), emphasizes evolution in the functional morphology and trophic ecology of gelatinous zooplankton. Biol Bull 219:249–267

Bayha KM, Graham WM (2014) Nonindigenous marine jellyfish: invasiveness, invasibility, and impacts. In: Pitt K, Lucas C (eds) Jellyfish blooms. Springer, Dordrecht, p 45–77

Benovi A, Justi D, Bender A (1987) Enigmatic changes in the hydromedusan fauna of the northern Adriatic Sea. Nature 326:597–600

Bowen BW, Gaither MR, DiBattista JD, Iacchei M and others (2016) Comparative phylogeography of the ocean planet. Proc Natl Acad Sci USA 113:7962–7969

Brodeur RD, Decker MB, Ciannelli L, Purcell JE and others (2008) Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. Prog Oceanogr 77: 103–111

Brotz L, Cheung WW, Kleisner K, Pakhomov E, Pauly D (2012) Increasing jellyfish populations: trends in large marine ecosystems. Hydrobiologia 690:3–20

Brown JH (1999) Macroecology: progress and prospect. Oikos 87:3–14

Condon RH, Graham WM, Duarte CM, Pitt KA and others (2012) Questioning the rise of gelatinous zooplankton in the world's oceans. Bioscience 62:160–169

Condon RH, Duarte CM, Pitt KA, Robinson KL and others (2013) Recurrent jellyfish blooms are a consequence of global oscillations. Proc Natl Acad Sci USA 110: 1000–1005

Cornils A, Wend-Heckmann B, Held C (2017) Global phylogeography of *Oithona similis* s.l. (Crustacea, Copepoda, Oithonidae) — a cosmopolitan plankton species or a complex of cryptic lineages? Mol Phylogenet Evol 107: 473–485

Costantini F, Rossi S, Pintus E, Cerrano C, Gili J, Abbiati M (2011) Low connectivity and declining genetic variability along a depth gradient in *Corallium rubrum* populations. Coral Reefs 30:991–1003

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nat Methods 9:772

Dawson MN (2005a) *Cyanea capillata* is not a cosmopolitan jellyfish: morphological and molecular evidence for *C. annaskala* and *C. rosea* (Scyphozoa: Semaeostomeae: Cyaneidae) in southeastern Australia. Invertebr Syst 19: 361–370

Dawson MN (2005b) Incipient speciation of *Catostylus mosaicus* (Scyphozoa, Rhizostomeae, Catostylidae), comparative phylogeography and biogeography in southeast Australia. J Biogeogr 32:515–533

Dawson MN, Hamner WM (2005) Rapid evolutionary radiation of marine zooplankton in peripheral environments. Proc Natl Acad Sci USA 102:9235–9240

Dawson MN, Hamner WM (2009) A character-based analysis of the evolution of jellyfish blooms: adaptation and exaptation. Hydrobiologia 616:193–215

Dawson MN, Jacobs DK (2001) Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). Biol Bull 200:92–96

Dawson MN, Martin LE (2001) Geographic variation and ecological adaptation in *Aurelia* (Scyphozoa, Semaeostomeae): some implications from molecular phylogenetics. Hydrobiologia 451:259–273

Dawson MN, Sen Gupta A, England MH (2005) Coupled biophysical global ocean model and molecular genetic analyses identify multiple introductions of cryptogenic species. Proc Natl Acad Sci USA 102:11968–11973

Dawson MN, Hays CG, Grosberg RK, Raimondi PT (2014) Dispersal potential and population genetic structure in the marine intertidal of the eastern north Pacific. Ecol Monogr 84:435–456

Dawson MN, Cieciel K, Decker MB, Hays GC, Lucas CH, Pitt KA (2015) Population-level perspectives on global change: genetic and demographic analyses indicate various scales, timing, and causes of scyphozoan jellyfish blooms. Biol Invasions 17:851–867

Doyle TK, Houghton JD, Buckley SM, Hays GC, Davenport J (2007) The broad-scale distribution of five jellyfish species across a temperate coastal environment. Hydrobiologia 579:29–39

Doyle TK, Hays GC, Harrod C, Houghton JD (2014) Ecological and societal benefits of jellyfish. In: Pitt K, Lucas C (eds) Jellyfish blooms. Springer, Dordrecht, p 105–127

Duarte CM, Pitt KA, Lucas CH, Purcell JE and others (2013) Is global ocean sprawl a cause of jellyfish blooms? Front Ecol Environ 11:91–97

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res 32:1792–1797

Excoffier L, Lischer HE (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol Ecol Resour 10: 564–567

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit 1 from diverse metazoan invertebrates. Mol Mar Biol Biotechnol 3:294–299

Gibbons MJ, Richardson AJ (2013) Beyond the jellyfish joyride and global oscillations: advancing jellyfish research. J Plankton Res 35:929–938

Glynn F, Houghton JD, Provan J (2015) Population genetic analyses reveal distinct geographical blooms of the jellyfish *Rhizostoma octopus* (Scyphozoa). Biol J Linn Soc 116:582–592

Gómez Daglio L, Dawson MN (2017) Species richness of jellyfishes (Scyphozoa: Discomedusae) in the Tropical Eastern Pacific: missed taxa, molecules, and morphology match in a biodiversity hotspot. Invertebr Syst 31: 635–663

Graham WM, Pagès F, Hamner WM (2001) A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451:199–212

Hallett BT, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71–75

Hebert PD, Ratnasingham S, deWaard JR (2003) Barcoding animal life: cytochrome *c* oxidase subunit 1 divergences among closely related species. Proc R Soc B 270(Suppl 1): S96–S99

Holland BS, Dawson MN, Crow GL, Hofmann DK (2004) Global phylogeography of *Cassiopea* (Scyphozoa: Rhizostomeae): molecular evidence for cryptic species and multiple invasions of the Hawaiian Islands. Mar Biol 145:1119–1128

Jaskuła R, Rewicz T, Płóciennik M, Grabowski M (2016). Pleistocene phylogeography of tiger beetle, *Calomera littoralis*, in North-Eastern Mediterranean and Pontic regions inferred from mitochondrial COI gene sequence. PeerJ 4:e2128

Kelly RP, Eernisse DJ (2007) Southern hospitality: a latitudinal gradient in gene flow in the marine environment. Evolution 61:700–707

Kogovšek T, Bogunovi B, Malej A (2010) Recurrence of bloom-forming scyphomedusae: wavelet analysis of a 200-year time series. Hydrobiologia 645:81–96

Kostylev VE, Erlandsson J, Ming MY, Williams GA (2005) The relative importance of habitat complexity and surface area in assessing biodiversity: fractal application on rocky shores. Ecol Complex 2:272–286

Krug PJ, Vendetti JE, Rodriguez AK, Retana JN, Hirano YM, Trowbridge CD (2013) Integrative species delimitation in photosynthetic sea slugs reveals twenty candidate species in three nominal taxa studied for drug discovery, plastid symbiosis or biological control. Mol Phylogenet Evol 69:1101–1119

Lawton JH (2000) Community ecology in a changing world. In: Kinne O (ed) Excellence in ecology, Book 11. International Ecology Institute, Oldendorf/Luhe

Lee PL, Dawson MN, Neill SP, Robins PE, Houghton JD, Doyle TK, Hays GC (2013) Identification of genetically and oceanographically distinct blooms of jellyfish. J R Soc Interface 10:20120920

Longhurst AR (2007) Ecological geography of the sea. Academic Press, Burlington, MA

Lucas CH, Dawson MN (2014) What are jellyfishes and thaliaceans and why do they bloom? In: Pitt K, Lucas C (eds) Jellyfish blooms. Springer, Dordrecht, p 9–44

Lucas CH, Jones DO, Hollyhead CJ, Condon RH and others (2014) Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers. Glob Ecol Biogeogr 23:701–714

Madin L, Deibel D (1998) Feeding and energetics of Thaliacea. In: Bone Q (ed) The biology of pelagic tunicates. Oxford University Press, Oxford, p 81–103

Marske KA, Rahbek C, Nogués-Bravo D (2013) Phylogeography: spanning the ecology-evolution continuum. Ecography 36:1169–1181

Menge BA, Daley BA, Lubchenco J, Sanford E and others (1999) Top-down and bottom-up regulation of New Zealand rocky intertidal communities. Ecol Monogr 69: 297–330

Miller B, Von der Heyden S, Gibbons M (2012) Significant population genetic structuring of the holoplanktic scyphozoan *Pelagia noctiluca* in the Atlantic Ocean. Afr J Mar Sci 34:425–430

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES science gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov 2010, New Orleans, LA. www.phylo.org/sub_sections/portal/sc2010_paper.pdf

Nagata RM, Moreira MZ, Pimentel CR, Morandini AC (2015) Food web characterization based on $\delta^{15}N$ and $\delta^{13}C$ reveals isotopic niche partitioning between fish and jellyfish in a relatively pristine ecosystem. Mar Ecol Prog Ser 519:13–27

Nychka D, Furrer R, Paige J, Sain S (2015) Fields: tools for spatial data. R package version 9.0. www.image.ucar.edu/fields

Oguz T (2005) Black sea ecosystem response to climatic teleconnections. Oceanography (Wash DC) 18:122–133

Ortman BD, Bucklin A, Pages F, Youngbluth M (2010) DNA barcoding the medusozoa using mtCOI. Deep Sea Res II 57:2148–2156

Paine RT (2010) Macroecology: Does it ignore or can it encourage further ecological syntheses based on spatially local experimental manipulations? Am Nat 176:385–393

Parsons T, Lalli C (2002) Jellyfish population explosions: revisiting a hypothesis of possible causes. Mer (Paris) 40: 111–121

Pitt KA, Welsh DT, Condon RH (2009) Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. In: Pitt KA, Purcell JE (eds) Jellyfish blooms: causes, consequences, and recent advances. Developments in Hydrobiology 206. Springer, Dordrecht, p 133–149

Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. J Mar Biol Assoc UK 85:461–476

Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Ann Rev Mar Sci 4:209–235

Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451: 27–44

Purcell JE, Malej A, Benović A (1999) Potential links of jellyfish to eutrophication and fisheries. In: Malone TA, Harding Jr LW, Smodlaka N, Turner ER. Ecosystems at the land-sea margin: drainage basin to coastal sea. Coastal and Estuarine Studies SS, Amorical Geophysical Union, Washigton, DC, p 241–263

Purcell JE, Brown ED, Stokesbury KDE, Haldorson LH, Shirley TC (2000) Aggregations of the jellyfish *Aurelia labiata*: abundance, distribution, association with age-0 walleye pollock, and behaviors promoting aggregation in Prince William Sound, Alaska, USA. Mar Ecol Prog Ser 195:145–158

R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/

R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, www.R-project.org/

Rambaut A (2002) Se-Al sequence alignment editor v2.0 software. University of Oxford. http://tree.bio.ed.ac.uk/software/seal/ (accessed on 15 February 2016)

Reum JC, Hunsicker ME, Paulsen CE (2010) Species composition and relative abundance of large medusae in Puget Sound, Washington. Northwest Sci 84:131–140

Reygondeau G, Maury O, Beaugrand G, Fromenti JM, Fonteneau A, Cury P (2012) Biogeography of tuna and billfish communities. J Biogeogr 39:114–129

Reygondeau G, Longhurst A, Martinez E, Beaugrand G, Antoine D, Maury O (2013) Dynamic biogeochemical provinces in the global ocean. Global Biogeochem Cycles 27:1046–1058

Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol Evol 24:312–322

Ricklefs RE (2008) Disintegration of the ecological community. Am Nat 172:741–750

Riddle BR (2016) Comparative phylogeography clarifies the complexity and problems of continental distribution that drove A. R. Wallace to favor islands. Proc Natl Acad Sci USA 113:7970–7977

Riginos C, Douglas KE, Jin Y, Shanahan DF, Treml EA (2011) Effects of geography and life history traits on genetic differentiation in benthic marine fishes. Eco-

graphy 34:566–575
Sanz-Martín M, Pitt KA, Condon RH, Lucas CH, Novaes de Santana C, Duarte CM (2016) Flawed citation practices facilitate the unsubstantiated perception of a global trend toward increased jellyfish blooms. Glob Ecol Biogeogr 25:1039–1049
Sax DF, Stachowicz JJ, Brown JH, Bruno JF and others (2007) Ecological and evolutionary insights from species invasions. Trends Ecol Evol 22:465–471
Schlitzer R (2015) Ocean Data View. http://odv.awi.de
Shanks AL (2009) Pelagic larval duration and dispersal distance revisited. Biol Bull 216:373–385
Sherman K (1991) The large marine ecosystem concept: research and management strategy for living marine resources. Ecol Appl 1:349–360
Spalding MD, Fox HE, Allen GR, Davidson N and others (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57:573–583
Sweetman AK, Smith CR, Dale T, Jones DO (2014) Rapid scavenging of jellyfish carcasses reveals the importance of gelatinous material to deep-sea food webs. Proc R Soc B 281:20142210
Swift HF, Daglio LG, Dawson MN (2016) Three routes to crypsis: stasis, convergence, and parallelism in the *Mastigias* species complex (Scyphozoa, Rhizostomeae). Mol Phylogenet Evol 99:103–115
Swofford DL (2002) PAUP*: phylogenetic analysis using parsimony (* and other methods). Version 4. Sinauer Associates, Sunderland, MA
Valentine JW, Jablonski D (2015) A twofold role for global energy gradients in marine biodiversity trends. J Biogeogr 42:997–1005
Villesen P (2007) FaBox: an online toolbox for FASTA sequences. Mol Ecol Notes 7:965–968
Winans AK, Purcell JE (2010) Effects of pH on asexual reproduction and statolith formation of the scyphozoan, *Aurelia labiata.* Hydrobiologia 645:39–52
Wright S (1965) The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 19:395–420
Young GA, Hagadorn JW (2010) The fossil record of cnidarian medusae. Palaeoworld 19:212–222

Editorial responsibility: Fabien Lombard (Guest Editor), Villefranche-sur-Mer, France

Submitted: April 24, 2017; Accepted: February 6, 2018
Proofs received from author(s): March 17, 2018