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MOLECULAR TOOLS

Population-level perspectives on global change: genetic and demographic analyses indicate various scales, timing, and causes of scyphozoan jellyfish blooms

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Abstract Whether a perceived increase in the abundance of jellyfishes is related to changing marine environments has been considered primarily using large-scale analyses of multi-species assemblages. Yet jellyfish blooms—rapid increases in the biomass of pelagic coelenterate species—are single-species demographic events. Using published and new genetic analyses and population surveys, we investigate whether there may be a critical knowledge gap between the scales of recent analyses and the scales of natural phenomena. We find that scyphomedusae may show population genetic structure over scales of tens to hundreds of kilometers, that environments vary regionally and locally, and that populations of medusae can display uncorrelated dynamics on these scales. These findings suggest genetic differences between populations and/or environmental differences between sites are important determinants of population dynamics in these jellyfishes. Moreover, the local abundance of medusae may be most strongly correlated with preceding rather than current local environmental conditions, indicating there is a cumulative time-course to the formation of 'blooms'. Broad-scale macro-ecological analyses will need to build from coordinated, long-term, fine-grained studies to synthesize, rather than mask, population-level phenomena in larger-scale analyses.

Keywords Climate · Discomedusae · Dispersal · Environmental change · Plankton · Scyphozoa

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Introduction

Whether a perceived increase in the abundance of jellyfishes is a consequence of changing marine environments often has been framed as a question requiring very large-scale analyses of multiple species (Purcell 2005; Richardson et al. 2009; Brotz et al. 2012; Condon et al. 2012, 2013). Yet an increase in the number or biomass of a pelagic coelenterate species—a 'jellyfish bloom'—is a "characteristic of … populations" (Graham et al. 2001:199), i.e., a demographic phenomenon (Lucas and Dawson 2014). While 'large' and 'population' scales are not necessarily mismatched analytically, they may be empirically, and it is timely to ask whether a critical gap in knowledge exists between the scales of recent analyses and the scales of natural phenomena.

Jellyfish blooms have been categorized either as a 'true bloom' if resulting from production and growth of new individuals, or as an 'apparent bloom' if resulting from redistribution of existing individuals (Graham et al. 2001). Although an apparent bloom most often will be preempted elsewhere by a true bloom, the distinction between 'true' and 'apparent' blooms is of some importance because it indicates the location, and possibly also timing, of the cause(s) of a jellyfish bloom (Lucas and Dawson 2014). The cause(s) of a true bloom occur(s), or occurred, at the site of the bloom; the cause(s) of an apparent bloom include(s), or included, event(s) elsewhere. For most blooms in most places, this spatio-temporal series of events remains largely unknown, but is essential to understanding the scales, timing, and causes of jellyfish blooms and whether or not they are 'invasive' sensu Valéry et al. (2008, 2009; see also "outbreak" sensu Richardson et al. 2009).

An allied issue is identifying the geographic scale at which jellyfish blooms occur. Elevated biomass of planktonic cnidarians has been reported across localized fronts (e.g., Brodeur et al. 1997; Purcell et al. 2000), within and between coastal lakes and fjords (Hamner and Hauri 1981; Lucas and Lawes 1998; Pitt and Kingsford 2000, 2003; Youngbluth and Båmstedt 2001), across bays and estuaries (e.g., Graham et al. 1992; Lucas et al. 1997), and in coastal shelf and midwater regions (e.g., Raskoff 2001; Suchman and Brodeur 2005; Decker et al. 2013); these studies often report temporal heterogeneity in abundance too. The spatial scales over which such variation in abundance reflects particular demographic events or demes, however, is uncertain. For example, information on the whereabouts of polyps and subsequent movements of ephyrae and medusa are for the most-part lacking.

Uncertainty about the provenance and extent of jellyfish abundances introduces ambiguity into efforts to describe jellyfish demographics and identify the causes of fluctuations. Analyses at single locations may not capture the full extent or time-course of demographic events nor discern among factors acting at larger scales (Decker et al. 2013; Lee et al. 2013; Lucas and Dawson 2014). Analyses that have aggregated data at the level of large marine ecosystems (LMEs; Brotz et al. 2012) or used primarily polyphyletic groups (e.g., Condon et al. 2013) to discern global trends, adopt shortcomings of the original studies and additionally may mask finer-scale spatial, temporal, and taxonomic variation in the occurrence of jellyfishes (and of other taxa in those datasets such as salps). Oversimplistic aggregation of data thus risks dissociating patterns of abundance from underlying biological, spatial, and temporal causes. Influences on marine and coastal systems that have been hypothesized to drive jellyfish dynamics—such as eutrophication, coastal development, alteration of large-scale ecosystem dynamics by over-fishing, inter-regional species introductions, and global climate change (Richardson et al. 2009; Duarte et al. 2012; Purcell 2012; Bayha and Graham 2014)—do vary spatially and temporally in their occurrences, intensities, and frequencies (Halpern et al. 2008, 2009). Even 'global' climate change has regionally differentiable environmental effects (Falvey and Garreaud 2009), and the global biodiversity crisis manifests through regional and local events (Opgenoorth and Faith 2013). The scales, strengths, transformations, and interactions of drivers of population dynamics of jellyfishes are uncertain.

Designing analyses that match the scales of pelagic coelenterate population dynamics with diverse putative causes thus remains largely unaddressed. Here, we explore a method that combines approaches from population genetics and population biology to identify genetic units, their spatial extent, their environments, and to determine whether distinct populations respond differently or similarly to which kinds of environmental variation (Lucas and Dawson 2014; see also e.g., Etterson and Shaw 2001; Both et al. 2006; Lehtonen et al. 2009; Pespeni et al. 2013). Our exploration is preliminary, limited to the five case studies—*Aurelia aurita*, *Catostylus mosaicus*, *Chrysaora melanaster*, *Mastigias papua*, and *Rhizostoma octopus*—for which both population biology and

population genetic data currently are available through a mixture of published and new analyses. In each case, we wish to answer the following four questions. Is there significant population genetic structure? On what spatial scales and how strongly are these jellyfish subdivided? Do genetically distinct populations have similar demographics? And, conversely, do all locations inhabited by the same population show the same dynamics? Based on the answers to those questions, we consider how to integrate the scale of jellyfish population dynamics analytically with the scales of putative causes, including global change.

Methods

Population genetics

Collection and phylogeographic analyses of *C. mosaicus*, *M. papua* and *R. octopus* are described by Dawson (2005a), Dawson and Hamner (2005), and Lee et al. (2013), respectively. Here, we summarize the subset of findings relevant to the current study (1) because they were used to decide the study design and (2) to distinguish this information from new results of this study.

Two clades, representing subspecies of *C. mosaicus* occur in southeastern Australia (Fig. 1) and within each of these clades there is statistically significant finer scale phylogeographic structure. For example, within the "Central" clade, comparison of Botany Bay and Lake Illawarra (NLI) leads to estimation of $\Phi_{ST} = 0.393$, a high degree of differentiation reflecting only a single shared allele (of nine total in both populations).

Mastigias papua in Palau form multiple geographically isolated populations within marine lakes (Fig. 2). Genetic comparisons among the three lakes considered here, for which there also are abundance data, reveal values of $\Phi_{ST} \geq 0.94$, reflecting zero alleles being shared between any pair of populations.

Rhizostoma octopus in the Irish Sea and adjacent areas has generally high haplotype diversity ($h \geq 0.667$) except in Tremadog Bay ($h = 0.396$) which also had lowest nucleotide diversity. There are three genetically distinct groups: (1) La Rochelle, (2) Tremadog Bay, and (3) Gormanstown, Rosslare, and Camarthen Bay (Fig. 3).

In addition, we conducted comparable analyses of new samples of *Aurelia aurita* and *C. melanaster* for this study. Oral arm tissue was clipped from 85 *A. aurita* at three locations—Horsea Lake, Beaulieu River, and Southampton Water (Fig. 4)—in southern England and two sites in the Irish Sea, all within its native range (Dawson et al. 2005). [To the best of our knowledge, all populations studied here are within species' native ranges Dawson 2005a, b)]. A $\sim$25 mm^3 piece of bell tissue was cut from 125 whole *C. melanaster* collected by surface and midwater trawls at eight stations south of 60°N during annual surface and midwater trawl surveys by NOAA Alaska Fisheries Science Center (see below for more details; Fig. 5). All tissue samples were preserved individually in 1–2 ml of 95 % ethanol, labeled, refrigerated, and later shipped to the University of California, Merced for storage at −15 °C and analyses.

DNA was extracted from the ethanol-preserved tissues using a CTAB-Phenol/Chloroform based protocol (Dawson et al. 1998). Cytochrome *c* oxidase subunit I (COI) was amplified using LCOjf (5′-ggtcaacaaatcataaagatattggaac-3′) and HCO2198 (Folmer et al. 1994) in PCRs consisting of six steps of 94 °C for 8 min, 51 °C for 2 min, 72 °C for 2 min, 94 °C for 4 min, 52 °C for 2 min, 72 °C for 2 min, then 33 cycles of 95 °C/45 s, 52 °C/45 s and 72 °C/60 s, followed by an extension step at 72 °C for 10 min; the reaction was terminated by cooling to 4 °C. Amplified COI fragments were purified using Qiagen (Valencia, CA) PCR clean-up columns, and prepared for sequencing in both directions using the PCR primers at the UC Berkeley DNA Sequencing Facility. Contigs were assembled and electropherograms were checked visually in SEQUENCHER v4.8 (GeneCodes, Ann Arbor, Michigan, USA), misreads corrected, and poorly resolved terminal portions of sequences discarded. The identities of sequences were confirmed by BLAST searching sequences in GenBank (Altschul et al. 1997), verifying the existence of open reading frames in amino acid translations using the invertebrate mitochondrial code in SEQUENCHER, and including sequences in preliminary phylogenetic analysis (e.g., with sequences from Bayha et al. 2010). Each species' COI sequences were aligned using CLUSTALX (Jeanmougin et al. 1998) and alignments checked by eye using amino acid translated sequences. All terminal positions with missing data were excluded from subsequent analyses.

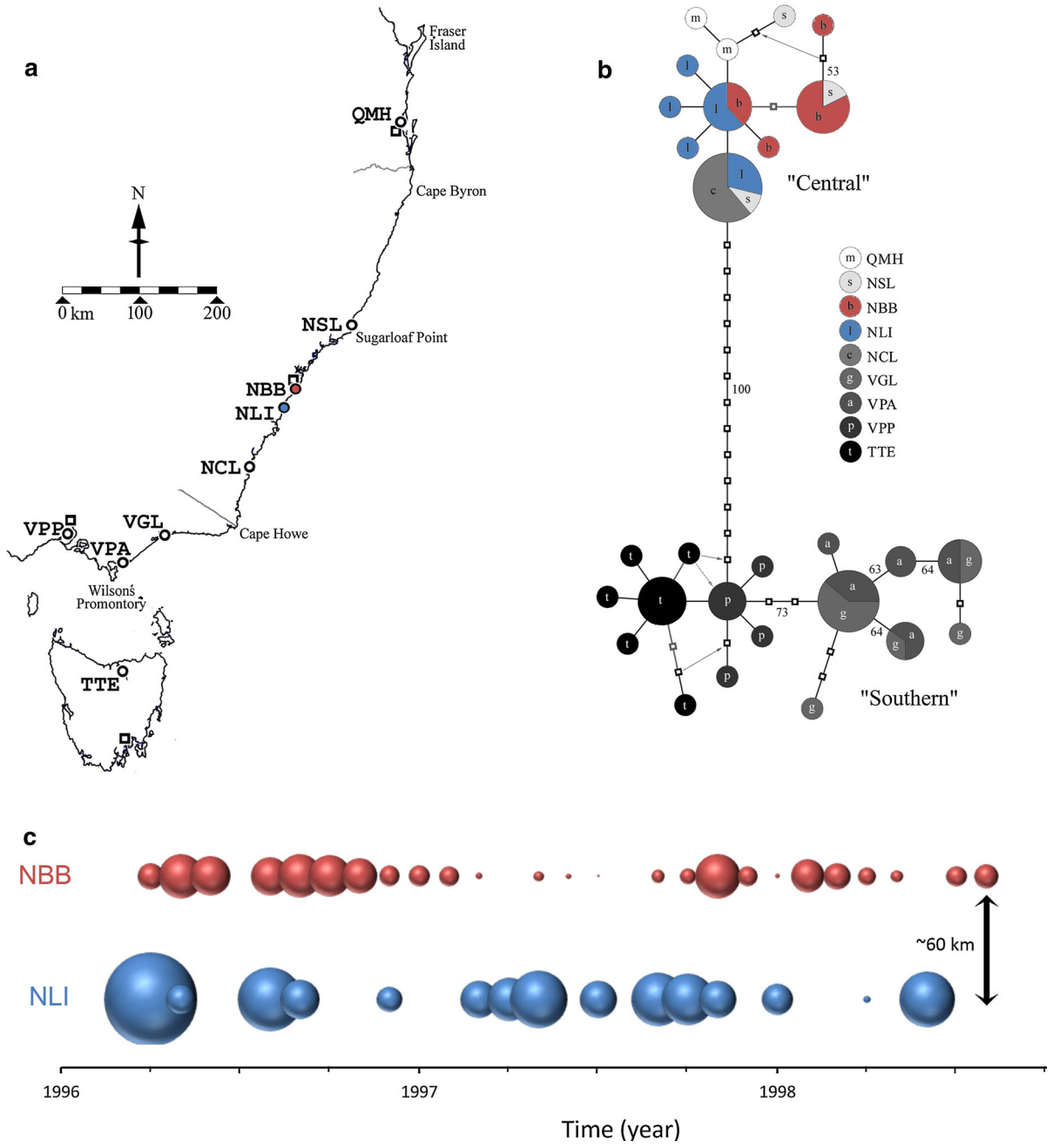

Fig. 1 **a** *Catostylus mosaicus* inhabit coastal lagoons and estuaries along the coast of southeastern Australia. **b** *C. mosaicus* are highly structured genetically, with distinct clades north versus south of Cape Howe, and distinct populations within each region; see Dawson (2005a, b, c) for details. *Colors* represent different locations, *circles* represent different alleles, the area of *circles* is proportional to the abundance of the allele, and *each line* of unit length between any *symbol* represents a single mutation. **c** The population dynamics of geographically proximate populations in Botany Bay (NBB) and NLI—here shown as changes in biomass—are uncorrelated; see Pitt and Kingsford (2000) for details. Different *colors* are used to represent locations inhabited by genetically distinct ($\Phi_{ST} \geq 0.2$) populations. The area of a *bubble* is proportional to the abundance of medusae

Gene and nucleotide diversity were calculated in Arlequin v.3.5.1.2 (Excoffier and Lischer 2010). To estimate population differentiation, we calculated Φ_{ST} values (10,100 permutations) using Arlequin. Significance levels were corrected for multiple tests using the sequential Bonferroni procedure (Rice 1989). Haplotype networks were reconstructed using statistical parsimony in TCS (Clement et al. 2000) or, for *C. melanaster*, using uncorrected pairwise sequence differences calculated in Arlequin as input for Haplotype Viewer (http://www.cibiv.at/~greg/haploviewer).

Population biology: abundance, biomass, and physical environment

Aurelia aurita, Southampton Water and Horsea Lake

Population dynamics of *A. aurita* were assessed in two locations in the Solent estuarine system on the south coast of the UK: (1) the productive estuary Southampton Water (50°51.36′N, 1°20.88′W) and (2) the semi-enclosed man-made Horsea Lake (50°49.32′N, 1°6.24′W). These two locations are within ~50 km of each other. Sampling in Southampton Water took place every 2 weeks between December 1992 and January 1995, and between February 1994 and January 1995 in Horsea Lake.

Collection of *A. aurita* medusae and environmental data (e.g., temperature, salinity) are fully described by Lucas and Williams (1994) for Southampton Water and by Lucas (1996) for Horsea Lake. Briefly, double-oblique hauls were made using 210 and 300 μm mesh cod-end plankton nets. *A. aurita* medusae were enumerated and bell diameter (BD) measured using a ruler. A YSI multiparameter probe was used to measure temperature, salinity and oxygen at 1 m depth intervals from the surface to 5 m.

Catostylus mosaicus, southeastern Australia

The population dynamics of *C. mosaicus* were assessed at Botany Bay (33°59′S, 151°11′E) and Lake Illawarra (NLI; 34°31′S, 150°50′E). Botany Bay was sampled approximately every 4–6 weeks from March 1996 until July 1998 and NLI was sampled approximately every 6–8 weeks from January 1996 to May 1998. Abundance of *C. mosaicus* was assessed using visual counts. The total numbers of medusae >50 mm BD were counted from the bow of a boat travelling at 10 kmh^{-1} along transects 1,500 m long, 3 m wide and 1 m deep. Numbers of medusae were counted along six transects at each of six sites within each location (i.e. $n = 36$). Current speeds at all locations were low and would have had a negligible effect on the length of transects. Counts were only made when the wind speed was <15 knots (kt) because wind-generated turbulence appeared to cause medusae to move deeper in the water column. At each location and time, the BD of 100 medusae was measured in situ by a diver at each of two sites (i.e. $n = 200$) to characterize the size distribution of the population.

The mode of the size distribution >50 mm BD was converted to wet weight (WW, grams) using $WW = 0.006 \times BD^{2.426}$ (Pitt and Kingsford 2003). The modal WW was then converted to carbon mass (mg) using the average C:WW ratio of 0.00947 for scyphozoan medusae (Lucas et al. 2011). The average carbon biomass density (mg C m^{-3}) per location was then estimated by multiplying the carbon biomass density by the average biomass density (number m^{-3}). Abundance and biomass per cubic meter are correlated ($p = 0.30$, $p = 0.022$, $n = 58$). Contemporaneous environmental data were unavailable.

Chrysaora melanaster, Bering Sea

Annual surface and midwater trawl surveys targeting forage fish were conducted by the NOAA Alaska Fisheries Science Center from 2004–2012 during August to October across the eastern Bering Sea. The sampling grid for the survey covered stations off the coast of Alaska, 159–174°W longitude and 54.5–64°N latitude. The surveys were conducted aboard contracted fishing vessels and the NOAA ship R/V Oscar Dyson. All tows were standardized for gear (50 m wide by 18 m deep) and duration of tow (30 min at 3.5–5 kt, covering 2.8–4.6 km). Jellyfish samples were collected using a midwater rope trawl, Model 400 (B.C. Cantrawl Pacific Limited). The rope trawl was 198 m long with nonuniform hexagonal mesh in the wings and body and a 1.2 cm mesh liner in the codend. All sampling was performed during daylight hours. Every medusa caught in the cod-end of the trawl net was sorted to species then enumerated.

Physical and biological oceanographic data were collected at each trawl station immediately prior to deploying the net. Vertical profiles of temperature, salinity, oxygen, chl *a* fluorescence, light attenuation

(beam c), and photosynthetically available radiation (PAR) were measured with a Sea-Bird Electronics Inc. Model 25 or Model 9 conductivity-temperature-depth profiler with ancillary sensors. We considered values averaged throughout the water column and also bottom temperature (5–10 m above the seafloor); the latter is correlated with medusae abundance in north and central (but not south) areas of the eastern Bering Sea (Decker et al. 2013). Water samples for nutrients (N, P, Si) and chl *a* (total and size fractionated) were collected at various depths using 5-L Niskin bottles. Data were subsampled for only the eight locations at which medusa were collected for genetic analyses.

Mastigias papua, Palau

Changes in the abundance of *M. papua* medusae were measured in three stratified marine lakes: Ongeim'l Tketau (OTM; 07°09.830′N 134°22.500′E), Ngermeuangel Lake (NLK; 07°19.400′N 134°30.507′E), and Goby Lake (GLK; 07°18.910′N 134°30.133′E). Physical characteristics of these lakes are described by Hamner and Hamner (1998). From December 2000 to January 2004, we quantified the abundance of medusae monthly using a 0.5 m diameter, 1 mm mesh net hauled vertically from the bottom of the mixolimnion to the surface. Net hauls were distributed evenly across the lake at 15 stations, and the set of 15 stations was sampled as many (two or three) times as possible during the course of 1 day. Each medusa was measured to the nearest 0.5 cm BD. Values reported are the mean estimated abundance of medusae in the lake each day surveyed.

Monthly, for the same period, we measured temperature, salinity and oxygen concentration at 1 m intervals from the lake surface to the bottom of the mixolimnion, at two sites per lake, with hand-held YSI 85 or Hydrolab Quanta meters. For each lake and sample date, we calculated the mean mixolimnion temperature (MMT; Martin et al. 2006), the mean mixolimnion salinity (MMS), and mean mixolimnion dissolved oxygen (MMO) also from 0 to 12 m.

Rhizostoma octopus, Irish Sea and adjacent areas

Estimates of jellyfish abundance were made during aerial surveys from an altitude of 152 m at a constant speed of 185 km h^{-1} (100 kt). Numbers of jellyfish observed within a 250 m observation strip each side of the aircraft were tallied every 5 min by each observer and combined to give an estimate of abundance (detailed methods are described in Houghton et al. 2006). Aggregations were mapped in the Irish Sea (51°12′N–55°04.8′N, 003°W–008°34.8′W) from June to October. Maximal abundance recorded on individual surveys was used to describe the prevalence of blooms each year.

We obtained sea surface temperature data for each 1° grid-square encompassing each bloom site from the International Comprehensive Ocean–Atmosphere Data Set (http://rda.ucar.edu/datasets/ds540.1/). This widely used data-set is formed by merging many national and international data sources that contain measurements and visual observations from ships (merchant, navy, research), moored and drifting buoys, coastal stations, and other marine platforms and thus provides comparable data among sites.

Synthesis

For each species, we ran parametric correlation analyses (Pearson's r) comparing changes in abundances among genetically distinct populations (i.e., $\Phi_{ST} \geq \sim 0.2$, which under a suite of simplifying assumptions approximates ≤ 1 migrant per generation) in Statistica v.7.1 (StatSoft Inc. 2006). For the datasets for which we also have environmental data, we investigated (1) contemporary correlations in a variable across sites, (2) contemporary correlations among all variables within each site, and (3) correlations between abundances of medusae in each genetically distinct population and (a) contemporary local environment and (b) local environment in preceding months. Positive autocorrelation within datasets will result in lower effective sample sizes (Fortin and Dale 2005:222) and lower power. We calculated the power (Fisher's z) for the relevant correlation coefficient *r* and sample size *n* of all statistical tests using the power analysis tool in Statistica v.7.1. Sequential Bonferroni adjustment (Rice 1989) was used to correct the α-level for multiple tests using the same dataset within species; our primary interest was in comparing relative effect sizes.

Results

Population genetics

Previously published genetic analyses of *A. aurita* (sensu stricto), *C. mosaicus*, and *M. papua* relevant to

this study are summarized in the "Methods" section (see also Figs. 1, 2, 3). The results of new analyses of *A. aurita* and *C. melanaster* follow.

Two genetically distinct groups of *A. aurita* occurred within our samples, one occupied the Irish Sea sites and another occurred in southern England (i.e. Southampton Water, Beaulieu River, and Horsea Lake); between-groups $\Phi_{ST} \geq 0.28$ ($p < 0.05$), and within-groups $\Phi_{ST} \leq 0.11$ ($p > 0.05$). Although haplotypes in these two populations occurred primarily in distinct clans (or 'haplogroups' Fig. 4), some haplotypes within Southampton Water and Horsea Lake were nested within haplotypes from the Irish Sea. Sequences are available in GenBank KJ026272–KJ026356.

Chrysaora melanaster has high haplotype richness ($h = 0.9824 \pm 0.0063$), modest differentiation among alleles ($\pi = 0.0064 \pm 0.0036$), and no phylogeographic structure in the southeastern Bering Sea (Fig. 5). Comparisons among all samples of *C. melanaster* medusae yield $\Phi_{ST} < \sim 0.09$ (statistically

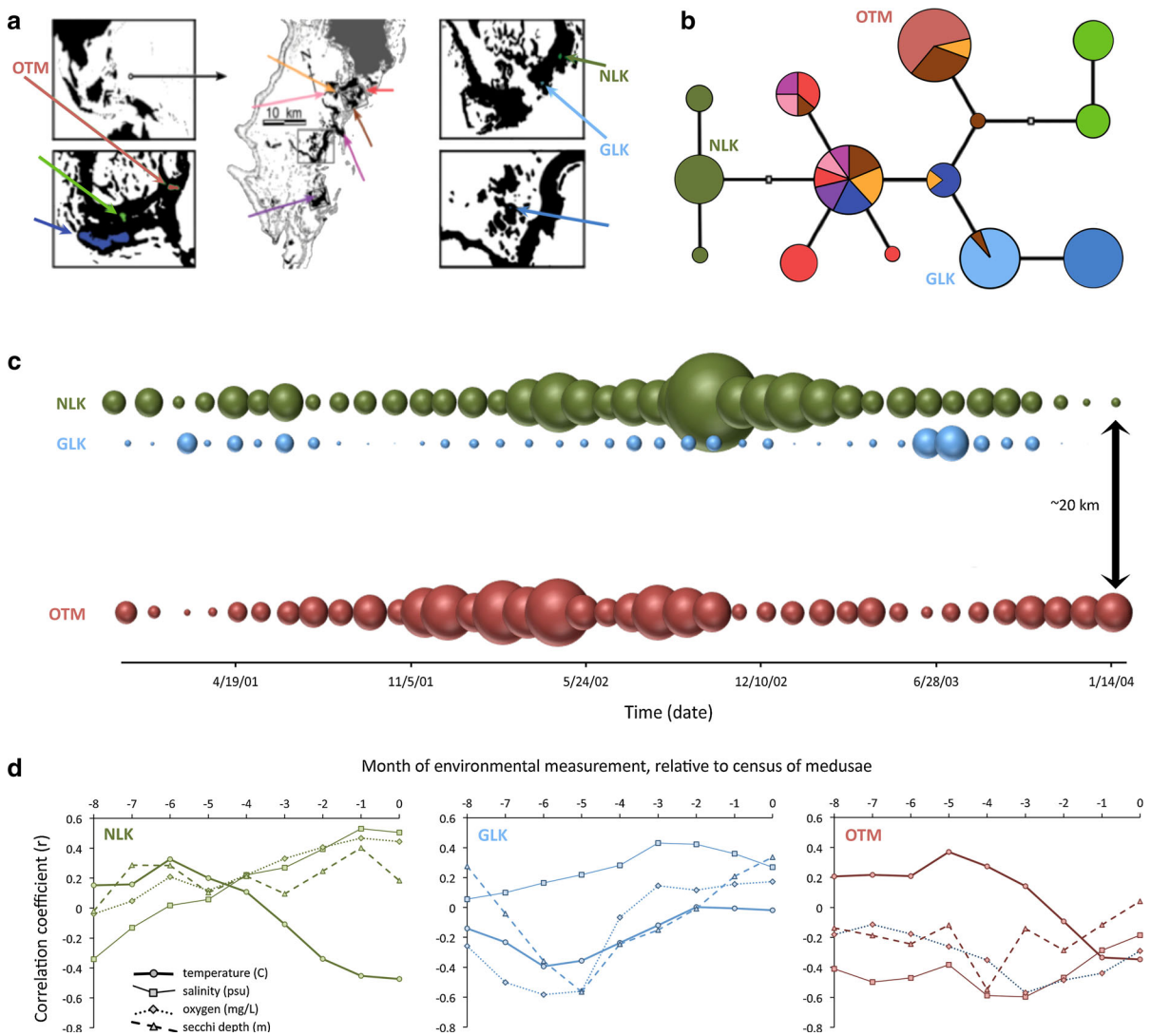

Fig. 2 **a** *Mastigias papua* inhabit coastal coves and marine lakes in Palau. **b** Animals in coves are genetically similar, whereas marine lakes harbor genetically distinct populations; see Dawson and Hamner (2005) for details. **c** The dynamics of populations in three lakes—OTM, NLK, and GLK—are weakly correlated ($r = -0.266 \leq r \leq 0.113$). **d** Abundances of *M. papua* in these three lakes show different strengths and timing of correlations with local environmental variation. The meaning of *symbols*, *shapes*, and *colors* is as described in Fig. 1

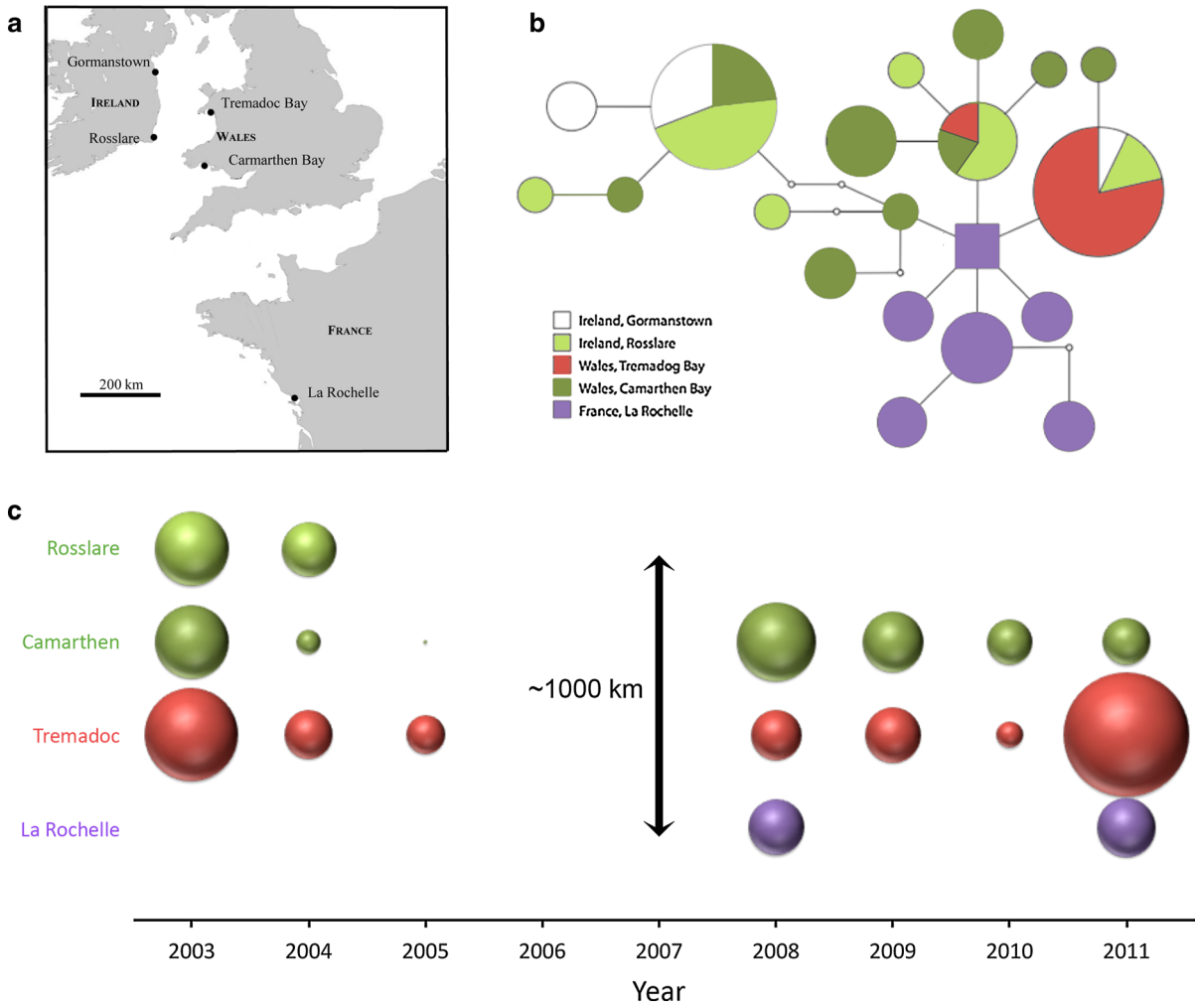

Fig. 3 **a** *Rhizostoma octopus* inhabit coastal embayments and open coastal areas in the northeastern Atlantic and adjacent seas and **b** are genetically connected or isolated as a function of landscape distance; see Lee et al. (2013) for details. **c** Annual abundances of medusae in four locations suggest mixed levels of spatial and temporal synchrony. The meaning of *symbols*, *shapes*, and *colors* is as described in Fig. 1

undifferentiable from $\Phi_{ST} = 0$). Sequences are available in GenBank KJ026148–KJ026271 (Figs. 2, 3, 4).

Population biology: abundance, biomass, and physical environment: and synthesis

Catostylus mosaicus, southeastern Australia

The maximum density of *C. mosaicus* medusae differs in Botany Bay and NLI, as does the timing of maximum and minimum densities. Changes in biomass of *C. mosaicus* medusa in Botany Bay and NLI do not co-vary (Pearson's $r = -0.004$, $p = 0.991$, $n = 13$; Fisher's $z = 0.05$; Fig. 1c). Environmental data were unavailable.

Mastigias papua, Palau

The monthly mean abundance of *M. papua* medusae varies almost threefold among marine lakes in Palau. Changes in abundances of *M. papua* medusae are not significantly correlated among lakes: GLK and NLK ($r = 0.113$, $p = 0.498$, $n = 38$; $z = 0.10$), GLK and OTM ($r = -0.208$, $p = 0.209$, $n = 38$; $z = 0.24$), or NLK and OTM ($r = -0.266$, $p = 0.106$, $n = 38$; $z = 0.37$).

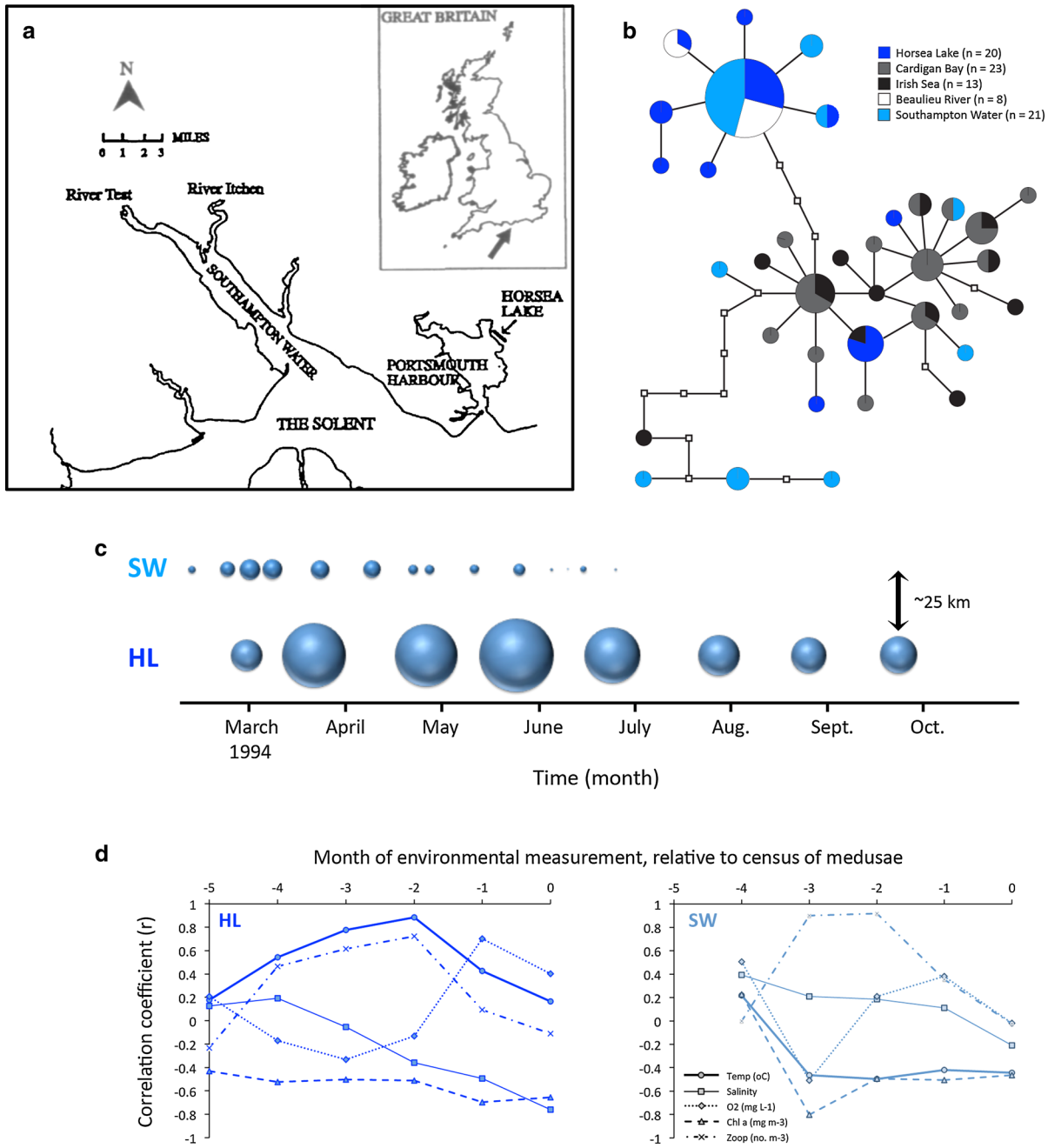

Fig. 4 **a** *Aurelia aurita* inhabit coastal waters in the Irish Sea, and estuaries and a man-made lake in southern England. **b** *A. aurita* in the southern England sites, Southampton Water and Horsea Lake, are genetically similar. **c** Annual abundances of medusae in these two locations are negatively correlated. **d** Despite differences in the population dynamics between sites, a strong correlation between medusae abundance and prey abundance 2–3 months prior emerges at both locations. The meaning of *symbols* and *shapes* is as described in Fig. 1; *shades* of *blue* are used to distinguish study sites that, in this case, are genetically similar. *Scale bar*: three miles is approximately 5 kilometers

Environmental characteristics show differing degrees of contemporary correlation among lakes; salinity is highly correlated across all lakes ($0.89 \leq r \leq 0.94$, $p < 0.001$, $n = 38$), temperature is moderately to strongly correlated with the stronger correlations between closer lakes ($0.59 \leq r \leq 0.81$, $p < 0.001$, $n = 38$; $0.98 \leq z \leq 1.00$), while dissolved oxygen and Secchi disc depth generally are not correlated among lakes [DO: $-0.08 \leq r \leq 0.06$, $p > 0.6$ ($z \leq 0.08$), except NLK vs OTM $r = 0.54$, $p \leq 0.001$ ($z = 0.95$), $n = 38$; Secchi: $-0.01 \leq r \leq 0.29$, $p \geq 0.07$ ($z \leq 0.07$), $n = 38$].

Within GLK, temperature, salinity, and DO were cross-correlated (magnitude $r \geq 0.41$, $p \leq 0.011$, $n = 38$; $z \geq 0.74$) but Secchi disk depth was uncorrelated ($-0.04 \leq r \leq 0.33$, $p \geq 0.04$, $n = 38$; $z \leq 0.54$). Within NLK, all environmental characteristics were consistently modestly cross-correlated (magnitude $r = 0.40$–0.61, $p \leq 0.013$, $n = 38$; $0.72 \leq z \leq 0.99$). Within OTM, temperature, salinity, DO, and Secchi disk depth were all uncorrelated ($-0.19 \leq r \leq 0.38$, $p \geq 0.02$, $n = 38$; $0.21 \leq z \leq 0.67$).

There were no significant correlations between contemporary medusae abundances and environmental parameters in GLK ($-0.02 \leq r \leq 0.34$, $p \geq 0.04$, $n = 38$; $0.05 \leq z \leq 0.56$) nor OTM ($-0.35 \leq r \leq 0.04$, $p \geq 0.03$, $n = 38$; $0.06 \leq z \leq 0.59$), but in NLK temperature, salinity and DO were each significantly correlated with medusae abundance (magnitude $r \geq 0.45$, $p \leq 0.005$, $n = 38$; $z \geq 0.83$). In the majority of cases medusae abundance was more strongly correlated with some aspect of preceding rather than contemporary environment (Fig. 2d).

Rhizostoma octopus, Irish Sea and adjacent areas

Annual abundance of *R. octopus* medusae varies approximately tenfold within and among sites. Changes in abundances of *R. octopus* medusae at Camarthen Bay and Tremadog, the two sites for which sufficient data exist, are uncorrelated ($r = 0.15$, $p = 0.74$, $n = 7$; $z = 0.06$). Visual inspection suggests abundances at other sites also are uncorrelated (Fig. 3). In contrast, environmental temperature is highly correlated among sites ($0.76 \leq r \leq 0.96$, $p \leq 0.001$, $n = 50$; $z \leq 1.00$). Medusae abundance and local temperature are uncorrelated at Camarthen ($r = -0.57$, $p = 0.18$, $n = 7$; $z = 0.30$) and at Tremadog ($r = 0.67$, $p = 0.10$, $n = 7$; $z = 0.43$); sample sizes were too small at Rosslaire and La Rochelle to include these locations in comparisons.

Aurelia aurita, Southampton Water and adjacent waters

The maximum density of *A. aurita* medusae differed approximately fivefold between Horsea Lake and Southampton Water; changes in abundance in the two locations are modestly negatively but not significantly correlated ($r = -0.47$, $p = 0.106$, $n = 5$; $z = 0.14$). Considering the same five contemporaneous sample dates, environmental variation at the two sites is highly correlated in terms of temperature ($r = 0.99$, $p = 0.001$, $n = 5$; $z = 0.99$) and uncorrelated in terms of salinity ($r = -0.74$, $p = 0.16$, $n = 5$; $z = 0.35$) and non-medusoid zooplankton abundance ($r = -0.61$, $p = 0.58$, $n = 5$; $z = 0.20$).

Within sites, more data were comparable. At Horsea Lake, temperature, salinity, DO, zooplankton abundance, and chl *a* concentration are statistically uncorrelated (range: $-0.60 \leq r \leq 0.34$, $p \geq 0.07$); sample sizes were ≥ 19 for all comparisons except any with DO ($n = 9$–10, leading to low power: $z = 0.49$ for the strongest correlation). In Southampton Water, temperature was modestly correlated with salinity, DO, and chl *a* only prior to Bonferroni correction (magnitude $r = 0.25$–0.52, $0.02 \leq p \leq 0.037$, $19 \leq n \leq 72$).

Considering all data available, correlations between contemporary medusae abundance and environmental characteristics at Horsea Lake were non-significant ($-0.26 \leq r \leq 0.40$, $p \geq 0.25$, $n_{temp} = 24$, $n_{sal} = 21$, $n_{zoo} = 23$, $n_{DO} = 9$, $n_{Chla} = 23$). Correlations between contemporary medusae abundance and environmental characteristics in Southampton Water were non-significant (magnitude $r \leq 0.25$, $p \geq 0.29$, $n_{sal} = 72$, $n_{zoo} = 23$, $n_{DO} = 19$, $n_{Chla} = 19$) except with temperature ($r = -0.32$, $p = 0.006$, $n = 74$; $z = 0.80$).

Considering the subset of years and months for which at least 4 contiguous months of data existed, slightly stronger relationships were evident, most notably in Horsea Lake, but medusae abundance usually was more strongly correlated with preceding than contemporary environment (Fig. 4d). Considering both sites, the most consistent and strong correlation was between medusae abundance and zooplankton density 2–3 months prior.

Chrysaora melanaster, Bering Sea

In the Bering Sea, *C. melanaster* are patchily distributed and thus abundance varies over 1,000-fold among sites within years; mean abundance of *C. melanaster* varies sixfold inter-annually (Fig. 5c). Correlations among environmental characteristics, considering all times for the locations for which genetic data are available, were weak ($-0.12 \leq r \leq 0.14$; $n = 55$–60 for each pairwise comparison; $0.14 \leq z \leq 0.19$). Correlations among medusae abundance and contemporaneous co-located environment characteristics also were weak ($-0.15 \leq r \leq 0.20$; $n = 54$ for each pairwise comparison; $0.19 \leq z \leq 0.31$). Mean and bottom water temperatures were not significantly correlated ($r = 0.05$, $p = 0.741, n = 54; z = 0.065$) and bottom temperature was not significantly correlated with medusae abundance ($r = -0.15$, $p = 0.267$, $n = 54$; $z = 0.19$) in this dataset; results for other variables are shown in Table 1.

Discussion

Whether a perceived increase in the abundance of jellyfishes (Condon et al. 2012) is correlated with changing marine environments (Halpern et al. 2008, 2009) has been considered generally in studies taking large-scale or global perspectives (e.g., Richardson et al. 2009; Brotz et al. 2012; Condon et al. 2012, 2013; Duarte et al. 2012; Purcell 2012) and occasionally including polyphyletic datasets (e.g., Condon et al. 2013, and to a lesser extent Duarte et al. 2012). Century-long global trends across such datasets are weak to non-existent (e.g., Condon et al. 2013); statistically significant trends (or trends in which there is high confidence)—increasing and decreasing—appear to emerge in recent decades globally (Condon et al. 2013; see also Brotz et al. 2012), in a minority of subregions (Brotz et al. 2012), and in a minority of individual datasets (Condon et al. 2013). The apparent long-term trends in jellyfish abundance are superimposed on decadal periodicity (Purcell 2012; Condon et al. 2013; Decker et al. 2014) and considerable interannual heterogeneity. Thus, the challenge for pelagic coelenterate ecology is how to extract general relationships representing causes and effects from complex natural data when links between inferred patterns and actual population dynamics and causes will be tenuous if care is not taken to address the appropriate scales of possible drivers and demographics. For example, 24 of the 37 long-term datasets considered by Condon et al. (2013), are multi-species datasets which may be driven by a single species, by different species at different times, or by all species in concert. On the other hand, five of the 13 single-species datasets considered the same species—*Pelagia noctiluca*—in different regions of the Mediterranean but did not assess whether these represented one (see Stopar et al. 2010) or more independent populations, although four show no long-term trend and the fifth showed a significant increase. Thus aggregate analyses may mask considerable variation attributable to functional and habitat differences among species or populations (see also Hallett et al. 2004), while failing to recognize the extent of populations could artificially inflate sample sizes.

Indeed, our initial exploration of the population biology and population genetics of five scyphozoans indicates that large-scale analyses that aggregate across locations and/or taxa will often mask considerable population-level variation. Of our five case-studies, three reveal significant population genetic structure on spatial scales of tens-to-hundreds of kilometers (*C. mosaicus, M. papua, R. octopus*). Of the four case-studies that also include abiotic data, temperatures and salinities across sites often were moderately to strongly correlated, consistent with regional climatic drivers, but other environmental parameters usually were weakly correlated across sites, suggesting locally determined dynamics. Correlations between abundances of conspecific medusae in genetically distinct populations and/or different locations were always weak and as often negative as positive. Moreover, the dynamics of populations may differ between species inhabiting exactly the same location (e.g., *M. papua* cf. *Aurelia* sp. 4 in OTM, Palau; this study cf. Patris et al. 2011).

Correctly identifying populations, therefore, enables us to more precisely posit links between cause and effect. For example, relatively cool, saline, well-oxygenated waters may favor high contemporary abundances of *M. papua* medusae in NLK, a relationship that does not emerge strongly in other lakes in Palau (but see Martin et al. 2006). More notable, perhaps, is that even though contemporary *M. papua* dynamics were uncorrelated across lakes in Palau, comparisons of timelines indicated that temperature is

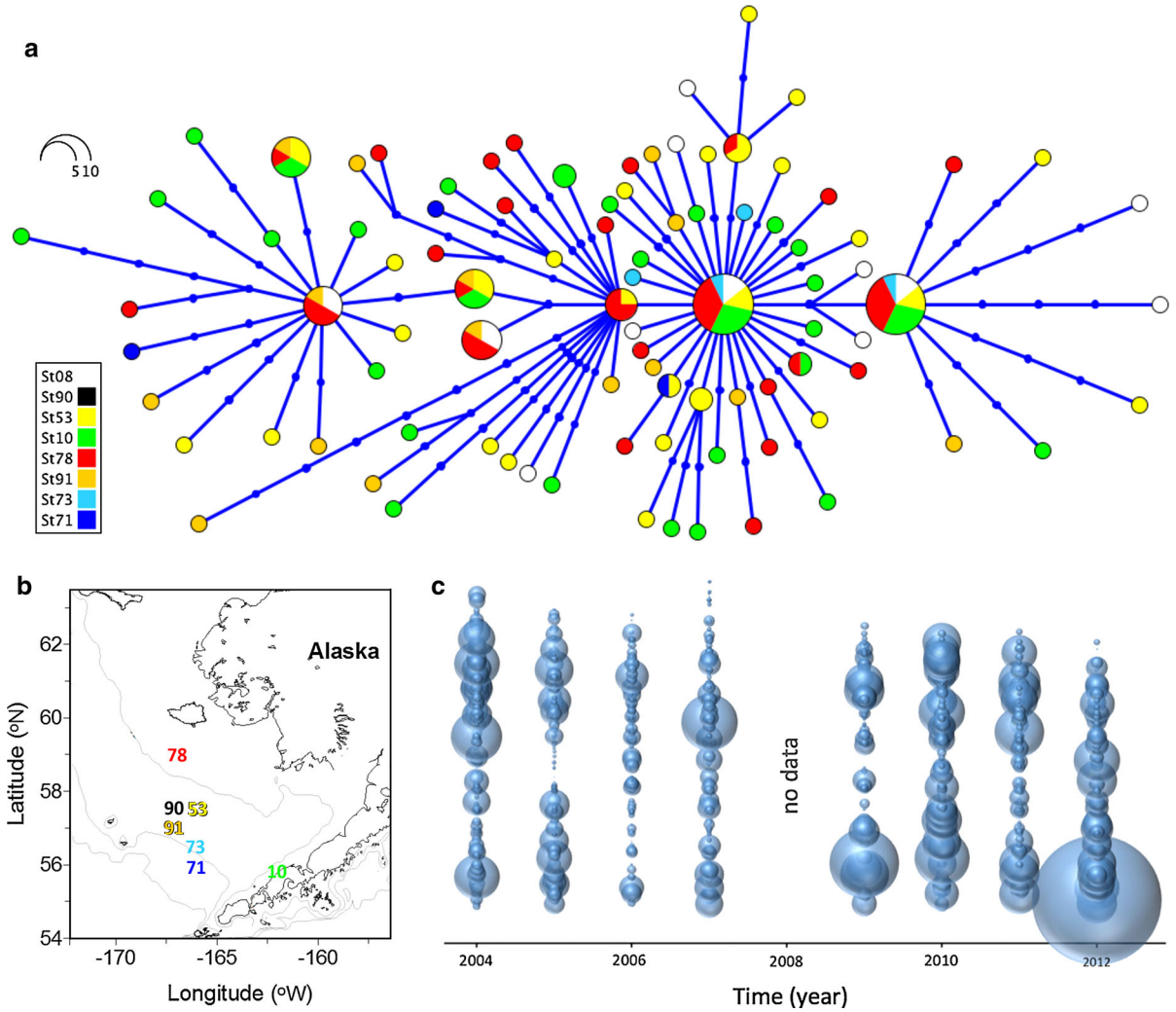

Fig. 5 **a** *Chrysaora melanaster* across in the southeastern Bering Sea are **b** genetically undifferentiated; *colors* are used to indicate different sites only. **c** Site-specific abundances of medusae vary by several orders of magnitude across locations within years, and mean annual abundances differ by up to an order of magnitude. The maximum linear distance separating locations is ~500 km. *Scale bar* three miles is approximately 5 kilometers

Table 1 Correlation coefficients among environmental characteristics and contemporary *C. melanaster* abundances based on data from eight sites in the eastern Bering Sea [including 'central' and 'south' regions of Decker et al. (2013)] at which genetically indistinguishable aggregations were sampled

	Temperature (Celsius)	Salinity (psu)	Oxygen (μmol/kg)	Chlorophyll *a* (μg/L)
Salinity (psu)	0.049			
Oxygen (μmol/kg)	0.140	−0.010		
Chlorophyll *a* (μg/L)	−0.119	−0.043	0.111	
Jellyfish (cpue)	0.198	−0.060	0.037	−0.005

Temperature is the mean water column temperature (see "Methods" for details). Sample sizes, *p* values, and power analyses are reported in the relevant subsection of "Results"

positively correlated with medusae abundance 5 or 6 months later, following a cooling trend, in both NLK and OTM (Fig. 2d). Similarly, even though the strength and timing of environmental factors and *A. aurita* dynamics varied across locations in southern England, a single factor—zooplankton abundance—was strongly implicated as acting in the same manner and with similar lag across locations (Fig. 4d). Jellyfish abundance also lags oceanographic conditions, in this case in the preceding year, in the eastern Bering Sea, where population size is influenced at least in part by advection across a broad shelf (Brodeur et al. 2008; Decker et al. 2013).

Our study indicates that genetic differences between populations and/or environmental differences between sites strongly influence population dynamics in these jellyfishes. Despite regional climatic forcing of local environmental characteristics such as temperature and salinity, presumably by seasonal and interannual variation in insolation and precipitation (e.g., by El Niño–La Niña; Martin et al. 2006), non-linear location-specific responses in these or other environmental characteristics appear to affect ecosystem dynamics substantially. Such population-level dynamics are the most direct indicators of the proximate mechanisms via which higher-level macro-ecological or regional patterns (e.g., Decker et al. 2014) must be mediated (e.g., see Hallett et al. 2004). To understand the effects of global change, therefore, it may be necessary to study local processes at many locations (for similar sentiments, see also e.g., Falvey and Garreaud 2009; Opgenoorth and Faith 2013) over appropriate intervals and durations.

We do not suggest that strong inferences can be made about specific causes of jellyfish population dynamics or their generality from this study. We have considered only five case studies, those for which some relevant data exist (see also Kogovšek et al. 2010; Stopar et al. 2010), which represents only a tiny percentage of pelagic coelenterate species, populations and locations. Also, mostly the original projects were of short duration, employed different study designs, and sometimes were of low power (e.g., our results for OTM cf. Martin et al. 2006). Moreover, all of our inferences are correlational and we have not considered laboratory or field-based manipulations that have the potential to establish cause and effect; larger-scale and longer analyses that might clarify the relative influence of regional climate signals also were not included. Environmental conditions are well known to influence demographic processes and our ability to show statistical links between the two is influenced by the temporal and spatial scales over which both are measured (e.g., Hallett et al. 2004), the relative strengths of intrinsic and extrinsic drivers (e.g., Grenfell et al. 1998), and can depend upon sufficient data and techniques (Hinder et al. 2012).

We do suggest that this population-level approach—which identifies the natural modules that permit independent tests of cause and effect—is generalizable and in fact necessary for studying jellyfish dynamics in changing coastal systems. Each population can be studied individually, in detail, and because a population study is a natural module it can be replicated and used in more complex studies that bridge scales. Such replicates are the foundation of purposefully designed 'natural experiments' that can test linkages between life-history stages, environments, places and times (see Lucas and Dawson 2014) using, for example, nested hierarchical designs and meta-analyses. This approach is essential because, like species-level responses to climate change which are heterogeneous (e.g., Parmesan and Yohe 2003; Perry et al. 2005; Parmesan 2006), it is now clear that population dynamics in jellyfishes can be influenced strongly by local processes despite global trends in climate change (as is the case in other taxa: Etterson and Shaw 2001; Both et al. 2006; Lehtonen et al. 2009; Pespeni et al. 2013). The five case-studies presented here, and other phylogeographic analyses (e.g., Dawson and Jacobs 2001; Holland et al. 2004; Dawson 2005c; Govindarajan et al. 2005), indicate that population genetic differentiation within jellyfish species may be commonplace. Biogeographic and oceanographic analyses show considerable variation in coastal environments and communities (Legaard and Thomas 2006, 2007; Blanchette et al. 2008). This combination of genetic and environmental differentiation provides opportunity for local adaptation (Sanford and Kelly 2011) which may manifest as idiosyncratic population dynamics. [We note also that local adaptation can manifest in fewer differences than might be expected, due to counter-gradient variation (Dawson and Martin 2001)]. Such local variation means that large-scale analyses which aggregate across locations and/or taxa can mask direct causal links and therefore alone will be insufficient to identify the causes of long-term trends. If we wish to

understand past and present changes, and to evaluate risks in the future, we need to design studies that reveal the scales of population genetic and demographic variation and to study dynamics across relevant scales (Harley et al. 2006; Franks and Hoffmann 2012) and timelines. As time-series of jellyfish populations increase in number and duration, our ability to discern causal links between population dynamics and environmental conditions over various scales will improve while also dealing with issues such as temporal autocorrelation within the time series (Hinder et al. 2012).

The generic claim that jellyfish are on the rise due to global change (e.g., Jackson 2008; Richardson et al. 2009) has long been considered oversimplistic (Mills 2001; Purcell 2005; Daryanabard and Dawson 2008; Condon et al. 2012; Gibbons and Richardson 2013; Decker et al. 2014; Lucas and Dawson 2014). Refocusing attention away from whether "the numbers of gelatinous zooplankton [are] rising in the world's oceans" (Condon et al. 2012) and toward discovering which species are on the rise, where, and why is overdue (Gibbons and Richardson 2013; Lucas and Dawson 2014); here we emphasize the importance of discovering which *populations* are on the rise (or otherwise), where, and why.

How to reframe the discussion and avoid pitfalls may in part be guided by reference to related fields. For example, fisheries biology has long tackled the difficult problem of identifying marine populations (Carvalho and Hauser 1995; Stokstadt 2010; Limborg et al. 2012), epidemiology and phylodynamics explore the origins, extent, causes, and severity of outbreaks (e.g., Grenfell et al. 2004), invasion biology's subject matter is 'outbreaks' and additionally provides cautionary tales about rhetoric and threshold criteria (Valéry et al. 2008, 2009; Davis et al. 2011), and biogeography is tackling integration of spatial and temporal scales (Dawson and Hortal 2012). Providing mechanistic answers requires the integration of long-term quantitative ecology—particularly population biology—and population genetics (Lucas and Dawson 2014) coupled with abiotic and biotic environmental measurements. Determining the causes of variation in the abundances of jellyfishes arguably is first the purview of ecological genetics (Urban 2008; Franks and Hoffmann 2012), which can provide information at the appropriate scales and resolution, and subsequently suited to macro-ecological meta-analyses of larger-scale and global patterns. A population perspective on global change encourages a productive balance between collection of detailed data and analyses of 'big data', and perhaps suggests a need for coordinated experimental networks (e.g., Adler et al. 2011) to complement sustained observational time-series (Fig. 5).

Conclusion

Scyphozoan populations span various spatial scales, from hundreds-of-meters to hundreds-of-kilometers, at least. The temporal dynamics of these populations may not be synchronized, even in closely related geographically adjacent populations. Discovering the causes of spatio-temporal variation in jellyfish abundances therefore requires studies of populations, from the smallest to largest scales. While recent aggregate analyses have attempted to investigate global patterns, they have not addressed the scales on which the causes of population dynamics occur and from which any larger patterns must emerge. The consequent gaps in knowledge, assumptions, and biases within those larger-scale analyses need to be redressed.

The key challenge is to integrate the scales of jellyfish population dynamics analytically with the scales of putative causes, from proximate events to global change. To meet this challenge, we need long-term studies of jellyfish densities and distributions replicated at the level of populations that are designed explicitly to address multiple multi-scale phenomena. Meta-analyses of population studies, which preserve the integrity of component modules as they are assembled into hierarchical datasets, present an unexplored opportunity.

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