Population Genomics of Marine Zooplankton

Chapter 19 in: *Population Genomics: Marine Organisms*
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19.1. Abstract

The exceptionally large population size and cosmopolitan biogeographic distribution that distinguish many – but not all – marine zooplankton species generate similarly exceptional patterns of population genetic and genomic diversity and structure. The phylogenetic diversity of zooplankton has slowed the application of population genomic approaches, due to lack of genomic resources for closely-related species and diversity of genomic architecture, including highly-replicated genomes of many crustaceans. Use of numerous genomic markers, especially single nucleotide polymorphisms (SNPs), is transforming our ability to analyze population genetics and connectivity of marine zooplankton, and providing new understanding and different answers than earlier analyses, which typically used mitochondrial DNA and microsatellite markers. Population genomic approaches have confirmed that, despite high dispersal potential, many zooplankton species exhibit genetic structuring among geographic populations, especially at large ocean-basin scales, and have revealed patterns and pathways of population connectivity that do not always track ocean circulation. Genomic and transcriptomic resources are critically needed to allow further examination of micro-evolution and local adaptation, including identification of genes that show evidence of selection. These new tools will also enable further examination of the significance of small-scale genetic heterogeneity of marine zooplankton, to discriminate genetic "noise" in large and patchy populations from local adaptation to environmental conditions and change.

Keywords: Zooplankton, Population genomics, Transcriptomics, Evolution, Population genetics

19.2. Introduction

II.A. Introduction to population genomics

Population genomic approaches entail simultaneous sampling of numerous variable loci within a genome and allow inference of locus-specific effects (Baird et al. 2008). These powerful new techniques are transforming our understanding of the population genetics, connectivity, demographic history, and local adaptation of marine organisms (Crawford and Oleksiak 2016; Pogson 2016). Genotyping hundreds to thousands of genetic markers for multiple individuals across populations or species has enabled identification of selectively-neutral markers that can be used for a wide variety of analyses (Luikart et al. 2003; Baird et al. 2008). Discrimination of statistical 'outlier' loci allows examination of the impacts of selection and evidence of local adaptation (Stapley et al. 2010). Whole-genome analysis of non-model organisms has enabled new insights into underlying evolutionary forces. However, significant challenges remain for whole-genome analysis of non-model organisms, thus necessitating and encouraging broad use of approaches that require little or no prior genomic data. These include reduced-representation genomic DNA libraries (Reitzel et al. 2013), genotyping-by-sequencing (Elshire et al. 2011), and exon-capture (Hodges et al. 2007; De Wit et al. 2015; Jones and Good 2016), although the latter requires prior knowledge of gene architecture. In broad view, population genomic approaches have enormous potential to yield significant new understanding of the ecological and evolutionary dynamics of zooplankton and other marine organisms.

19.2.1. Introduction to marine zooplankton

19.2.2.1. Biodiversity: The marine zooplankton assemblage includes ~6,000 described species of holoplanktonic metazoan organisms that complete their entire cycle in the water column (Wiebe et al. 2010). The phylogenetic diversity of this assemblage is impressive, with 11 phyla and 27 orders represented (Bucklin et al. 2010b). However, these numbers most likely markedly underestimate the actual biodiversity – perhaps by several orders of magnitude – due to the presence of cryptic variation within geographically widespread species or sibling species swarms, as well as undiscovered species in

under-sampled or explored habitats (Bucklin et al. 2010a; Beaugrand 2017). Molecular approaches, including DNA barcoding and metabarcoding, are providing important new insights into this 'hidden diversity' of marine zooplankton (Lindeque et al. 2013; Bucklin et al. 2016).

19.2.2.2. Biogeography: Global patterns of zooplankton biogeographic distributions have been well-characterized for the epipelagic (0 – 200 m) zone (Longhurst 2007). The many classical studies form a basis for ongoing examination of climate-driven range changes and regime shifts (deYoung et al. 2008). In contrast, the deep ocean, including the mesopelagic (200 – 1,000 m) and bathypelagic (1,000 – 4,000 m), remains under-sampled and poorly-known (but see Wiebe et al. 2010; Laakmann et al. 2012). Many species exhibit cosmopolitan distributions, with ranges spanning multiple ocean basins and broad latitudinal ranges (Peijnenburg and Goetze 2013). However, there are many exceptions to this oversimplified description, likely resulting from specific habitat requirements, restricted gene flow, or relict populations (Chust et al. 2016). Further complicating analysis of species distributional patterns are rather characteristic high ratios of local-to-global species diversity; a net sample from oceanic waters may contain hundreds of species of copepods or ~10% of the global total (Kuriyama and Nishida 2006).

19.2.2.3. Life history: Many zooplankton species have life histories entailing multiple stages with different micro-habitat preferences and requirements. Some exhibit alternation of sexual and asexual generations. Most are relatively short-lived organisms, with generation spans from several months to a couple of years. As a group, marine zooplankton are useful indicators of impacts of environmental variability or climate change, since they are rapid-responders in terms of species distribution and abundance. The exceptional diversity of marine zooplankton – in terms of phylogenetic biodiversity, pelagic biogeography, and life history variation – provided a unique opportunity to examine ecological and evolutionary genomic responses. This review will summarize new knowledge resulting from population genomic examination of the genetic diversity and structure, phylogeography and connectivity, demographic history, and local adaptation of marine metazoan holozooplankton.

19.2.3. Genomic resources for marine zooplankton

19.2.3.1. Published genomic resources: It can be argued that there are no universally-accepted model species among the marine zooplankton; in many cases, there are no closely-related model organisms to which extrapolations or comparisons can be made (Ellegren 2014). However, the number of marine zooplankton species targeted for genome-scale studies is growing, including species ranging phylogenetically from the Cnidaria to the Urochordata and including ecologically-important or keystone species for some pelagic ecosystems, such as the Southern Ocean salp, *Salpa thompsoni* (Jue et al. 2016) (Table 1).

For the most part, marine zooplankton species targeted for reference sequencing and assembly have been identified by their impact to ongoing comparative genomic studies or as part of larger genome consortia. An example of this latter group is the genome sequence for the copepod *Eurytemora affinis*, a species targeted for sequencing as part of the i5K Pilot Project aimed at sequencing 28 arthropod genomes (i5K Consortium 2013; Eyun et al. 2017). Currently, assembled genomes are available for species representing only a snapshot of some of the major lineages of eukaryotes and a small sampling of the species diversity of the pelagic realm (Table 1). A significant factor in the identification of a target species for a genome assembly effort is the estimated genome size. Notably, all the reference genomes available are from organisms whose genome size estimates are significantly smaller than 1GB, presumably since the depth of coverage required is low enough to represent a feasible investment of resources in terms of fiscal and computational effort. While reference quality assemblies are ideal (e.g., *Oikopleura dioica*, Denoeud et al. 2010), lower coverage assemblies can still provide a high enough N50-value (i.e., the weighted median statistic such that 50% of the entire assembly is contained in contigs or scaffolds equal to or larger than this value) to afford extensive gene predictions (e.g., Jue et al. 2016).

Recently, mining genome databases such as NCBI and the SRA (Short Read Archive) for partial genome sequences has afforded broader comparisons among species lacking a fully assembled genome. For example, a newly derived reference for the common estuarine copepod *E. affinis* was compared to

short read genomic sequence data from two other copepods, the freshwater cyclopoid copepod, *Mesocyclops edax* (SRX246444 and SRX246445; Sun et al. 2014) and the North Atlantic copepod, *Calanus finmarchicus*) (SRX456026; Smolina et al. 2014), revealing species-specific adaptations of the chemosensory related gene families to environments (Eyun et al. 2017).

19.2.3.2. Genome size in the zooplankton: The average estimated genome sizes (haploid nuclear DNA contents) of holoplankton species are in general far above 1 GB (Fig. 1) and varies more than 900-fold, from 0.07 GB in *Oikopleura dioica* (Appendicularia) to 63.2 GB in *Ampelisca macrocephala* (Amphipoda). Variation of genome sizes in marine zooplankton is especially large within the Copepoda with > 370-fold variation among species (Leinaas et al. 2016; Madoui et al. 2017) followed by Ostracoda and Malacostraca with around 80-fold and 70-fold variation of genome size among species, respectively (Gregory 2017; Jeffery et al. 2017). To date, genome size has been investigated for 115 species of zooplankton, with poor representation of important phyla, including Chaetognatha, Cnidaria, Ctenophora, Mollusca and Chordata.

Several trends or patterns are emerging from genomic analyses of crustaceans, although only a few species have been studied to date. First, a positive relationship between genome size (C-value) and body size has been observed in copepods (McLaren et al. 1988; Wyngaard and Rasch 2000), amphipods (Hessen and Persson 2009), and ostracods (Jeffery et al. 2017). However, there is considerable variability in genome size both among species of similar body size (Gregory et al. 2000; Leinaas et al. 2016) and within species due to environmental conditions (McLaren et al. 1988; Escribano et al. 1992; Leinaas et al. 2016). Second, genome size has been associated with specific habitats and environmental conditions. Marine crustaceans are likely to have larger genomes than freshwater and terrestrial ones (Jeffery 2015; Alfsnes et al. 2017); within the marine realm, polar species tend to have larger genomes compared to temperate species (Hessen and Persson 2009; Jeffery 2015; Leinaas et al. 2016). Jeffery (Jeffery 2015) hypothesizes that such large genomes may result from the expansion of transposable elements and other repetitive elements, due to relaxed selection for rapid development or reduced constraints on body size in

predictable and stable marine polar environments, compared to more fluctuating environments.

Causes and mechanisms of genome size variability and particularly expansion of genome sizes are still not known. Among eukaryotes, genome size is positively correlated with gene number, average intron size, and number of introns per genome (Elliott and Gregory 2015). The main drivers of genome size expansion are suggested to be whole-genome duplication (polyploidization) or partial duplication events and proliferation of noncoding elements (Dufresne and Jeffery 2011).

Information on genome size, genome sequence, and karyotype is sparse in marine zooplankton, limiting our understanding of genome evolution. Nevertheless, evidence from insects and crustaceans suggest that accumulation of transposable and repetitive elements may be the primary contributor to their large genome sizes (Alfsnes et al. 2017), while polyploidization is probably not the most common driver of genome evolution in zooplankton (Gregory and Hebert 1999). For example, species of the copepod genera *Calanus* and *Pseudocalanus* exhibit quantum shifts in genome size (C-values) within each genus, but share similar chromosome complements (McLaren et al. 1989).

Partial duplication or amplification of genomic regions may be common in large genomes of zooplankton, particularly for ribosomal rDNA and protein-coding genes. Among eukaryotes, rDNA copy number correlates positively with genome size (Prokopowich et al. 2003). For species of *Calanus*, 18S rDNA gene copy number has been found to approximately double between *C. finmarchicus* (15,300 copies; 2C = 12.95 pg) and *C. glacialis* (33,500 copies; 2C = 24.20 pg; Wyngaard et al. 1995). Transcriptomic analysis has indicated the presence of multi-copy gene families originating from multiple duplications of an ancestral gene in copepods (Lenz et al. 2014; Yang et al. 2014), euphausiids (Toullec et al. 2013; Sales et al. 2017), and pteropods (Maas et al. 2015; Thabet et al. 2017).

19.2.3.3. Mitochondrial genomes: Fragments of mitochondrial DNA were among the first molecular tools used to tackle questions related to zooplankton species identification, phylogenetics, phylogeography, and population genetics. For example the cytochrome oxidase sub-unit I is preferentially used as a barcode for metazoan (Schindel and Miller 2005), and has been used frequently

for marine zooplankton (Bucklin et al. 2007, 2010a, 2011; Blanco-Bercial et al. 2014).

Recent technological advances are allowing routine sequencing of whole mitochondrial genomes (mitogenomes), with marked increase in the power of phylogenetic and phylogeographic analyses compared to use of short mtDNA sequences. Applications such as shotgun sequencing on genomic DNA using high throughput sequencing technologies afford opportunities to capture other genomes that may be resident within a sample, such as mitochondrial DNA. Given the smaller target genome size (12-20KB), mitogenomes are easier to subsample from larger datasets or to assemble using a PCR-build approach (Maricic et al. 2010; Hahn et al. 2013; Kollias et al. 2015).

Mitogenomics is a promising field of research that will contribute new insights into the phylogenetic history and evolution of planktonic species. For example, sequencing the mitogenome of the chaetognath, *Spadella cephaloptera*, allowed resolution of the phylogenetic position of the chaetognaths within Protostome lineages (Papillon et al. 2004). Only a few mitogenomes have been published thus far – especially when the species diversity of zooplankton is considered – and within those, unexpected features appear to be more common than previously thought. Mitogenomes are publicly available for a number of ecologically-important species representing diverse phylogenetic lineages of marine zooplankton (Table 2), and additional complete mitochondrial assemblies may be found within incompletely-explored genomic data. Nonetheless, the sequencing and assembly of complete mitogenomes of marine zooplankton species has progressed at a much slower pace than other for vertebrate groups (Genome 10K Community of Scientists 2009; GIGA Community of Scientists 2014).

In animals, the mitogenome is relatively well conserved, with 36 or 37 genes, including two for rRNAs, 22 for tRNAs and 12 or 13 for protein-coding genes. The mitogenomes available for marine zooplankton species indicate a general trend of high intra- and interspecific variability. Rearrangement of gene order is exceptionally common and has been documented in amphipods (Ki et al. 2010) and ctenophores (Kohn et al. 2012), with some of the genes relocated to the nuclear genome (Pett et al. 2011). Copepods also show marked variability among congeneric species and among genera (Fig. 2; Jung et al.

2006; Minxiao et al. 2011). The most exceptional cases of mitochondrial variability documented to date are in the chaetognaths, *Spadella cephaloptera* and *Sagitta elegans*, for which natural populations exhibit unprecedented levels of intra-specific divergence (Marlétaz et al. 2017).

The variability observed in the mitogenomes of different species/lineages is also apparent in the genes content and size of these mitogenome (Table 2). The smallest mitogenome reported is the ctenophore, *Mnemiopsis leidyi*, with only 10 kb, which is missing 25 genes (Pett et al. 2011). Within the chaetognaths, mitogenomes are also very reduced compared to other metazoans, missing several common genes (Helfenbein et al. 2004; Papillon et al. 2004). On the other hand, the longest mitogenomes documented belong to the Copepods, up to 20 kb (Minxiao et al. 2011). Several mitogenomes were found to contain multiple copies of some sequences (Ogoh and Ohmiya 2004; Burton et al. 2007), or short tandem repeats, similar to microsatellites (Shen et al. 2011).

19.2.3.4. Transcriptomic resources: For some species, especially those with large, duplicated and/or evolutionarily-divergent genomes, analysis of transcriptomes has proven more feasible, accurate and cost-effective (De Wit et al. 2016). Transcriptomic data have the further advantage of allowing identification and annotation of target genes used in the examination of genomic micro-evolution and local adaptation (Havird and Santos 2016). Transcriptomic data, including partial reference transcriptomes are available for a number of marine zooplankton species (Table 3).

19.3. Applications of population genomics for marine zooplankton

19.3.1. Population genetic diversity and structure

Although many zooplankton species exhibit broad geographic distributions and appear to have high dispersal potential, both biological and physical environmental processes may limit gene flow. Previous studies have revealed significant genetic differentiation of geographic populations of marine organisms over a range of spatial scales (Hellberg 2009; Weersing and Toonen 2009). Two general principles may be gleaned from many studies of zooplankton population genetics: first, zooplankton are quite variable in many different molecular characters; second, this variability is resolved into genetically-

divergent, geographically-distinct populations for only some species and at some temporal and spatial scales (Peijnenburg and Goetze 2013).

Ocean processes that are thought to be significant for population genetic structuring of zooplankton are currents, persistent eddies, ocean gyres and other physical ocean structures at the mesoscale (10s to 100s km) to large scale (100s to 1000s km). The physical structure of the ocean can alter the timing of reproduction and mortality events, providing biological barriers to gene flow. Geological features – continents, islands and other landforms, continental shelves, seamounts, and ocean ridges – may form natural barriers to dispersal. In contrast, cosmopolitan species, which range from 40^{o}N to 40^{o}S and are found in every ocean basin, may have few barriers to dispersal throughout their range. These species may exhibit large-scale spatial population genetic structure due to isolation by distance (i.e., reproductive isolation resulting when the geographic range of the species far exceeds the dispersal potential of an individual).

The temporal stability of population genetic diversity and structure is an important consideration and useful metric. Since zooplankton are subject to transport in ocean currents, temporal stability of population genetic characters may indicate retention of local populations or local recruitment. An unfortunate aspect of many studies of zooplankton populations is the collection of samples from different regions during different years, thus confounding spatial and temporal variation. In relatively few studies, spatial and temporal contributions to population genetic structure have been analyzed separately using appropriately-collected samples (Goetze et al. 2015; Iacchei et al. 2017).

Patterns of genetic diversity and structure have been examined over a wide range of spatial scales for species representing many lineages of the zooplankton assemblage. Some species have been shown to be panmictic, such as *Pelagia noctiluca* (Stopar et al. 2010) and *Euphausia superba* (Deagle et al. 2015). Many species exhibit geographic variation reflecting geographic barriers and/or circulation patterns: e.g., *Tigriopus californicus* (Renaut and Dion-Côté 2016), *Eukrohnia hamata* (Kulagin et al. 2014), and *Caecosagitta macrocephala* (Miyamoto et al. 2010), to name a few. A number of species show large-

scale patterns of genetic diversity associated with latitudinal gradients (e.g., Francisco et al. 2014) and among ocean basins, including *Eukrohnia hamata* (Miyamoto et al. 2012), *Pleuromama abdominalis* (Hirai and Tsuda 2015), and *Oithona similis* (Cornils et al. 2017).

The occurrence and significance of small-scale genetic patchiness in marine zooplankton populations remain a subject of study and disagreement. Such variability has been considered to reflect the genetic "noise" of large and under-sampled populations of copepods (e.g., Goetze et al. 2015). Small-scale heterogeneity was considered to reflect advective transport from diverse recruitment sources in the Antarctic krill, *Euphausia superba* (Batta-Lona et al. 2011).

Due to nearly-universal application in population genetic studies, hierarchical analysis of variance using Wright's *F*-statistics related measures (Excoffier et al. 1992) provides useful benchmarks for comparisons among species, regions, and environments. However, *F*-statistics have assumptions that are surely not met for zooplankton (Hellberg 2009), including genetic equilibrium conditions, symmetrical migration, and stable populations. The usefulness of *F*-statistics is further limited by the very large population sizes of many zooplankton, which result in relatively larger confidence intervals for very small *F* values (Waples 1998), and thus a lack of statistical significance for high gene flow species (see Waples et al. 2008). At least partly for this reason, population genetic studies of marine species have also employed various measures of oceanographic distance (Hansen and Hemmer-Hansen 2007; McGovern et al. 2010; Alberto et al. 2011; Schunter et al. 2011) and approaches such as seascape genetics (Galindo et al. 2010).

Until recently, population genetic studies have most frequently been conducted with markers representing a very small fraction of the genome, such as individual mitochondrial or nuclear genes and microsatellites (see reviews by Avise 2009; Hellberg 2009; Peijnenburg and Goetze 2013). Rates of divergence and amounts of variation differ among these markers, but many studies have documented significant genetic differentiation of zooplankton populations at large, ocean basin scales using mitochondrial DNA (e.g., Goetze 2005; Goetze and Ohman 2010; Miyamoto et al. 2010; Blanco-Bercial

et al. 2011a; Miller et al. 2012; Norton and Goetze 2013; Dawson et al. 2015) and microsatellite markers (Bolte et al. 2013; Andrews et al. 2014). A number of studies have used mitochondrial DNA markers to resolve population structure of zooplankton populations associated with physical barriers to gene flow, including ocean circulation, for copepods (Aarbakke et al. 2011; Blanco-Bercial et al. 2011b, 2014) and euphausiids (Bucklin et al. 1997; Zane et al. 1998, 2000; Zane and Patarnello 2000; Papetti et al. 2005; Patarnello et al. 2010).

Both mitochondrial and microsatellite markers continue to be widely used for population genetic analysis of zooplankton, allowing useful comparisons among diverse species and ocean environments. Studies using single markers have limitations, not least that results may differ among studies using different markers (Avise et al. 2016). In addition to their limited analytical power, studies using multiple markers can yield discordant conclusions. In particular, the haploid nature and uniparental inheritance of mitochondrial markers, and consequent smaller effective population size, may generate differences from results using nuclear markers (Toews and Brelsford 2012).

Population genomic approaches can also be used for phylogeographic analysis (i.e., the description of the geographical distributions of the genetic lineages within a population or species; Avise 2009; Avise et al. 2016). Such analysis allows for the characterization of dispersal and quantitative estimation of the rate and direction of exchange among populations. Recent reviews of larval dispersal and population connectivity (Cowen and Sponaugle 2009) and gene flow (Hellberg 2009) in the ocean have provided comprehensive assessment and analyses for marine organisms. Quantitative estimates of population persistence and directional (asymmetric) migration can also entail approaches that are less sensitive to lack of population stability and non-equilibrium conditions, typical of marine organisms (Knowles 2009). Analysis of patterns and pathways of gene flow has revealed that patterns of population connectivity of marine organisms do not always mimic major ocean currents (Kool et al. 2013; Riginos et al. 2016), even for zooplankton (Blanco-Bercial and Bucklin 2016; Questel et al. 2016).

Phylogeographic analysis can also provide a window into the evolutionary history of a population

or species. Results can be interpreted to estimate and understand the age of the lineage in terms of time to coalescence (i.e., the common ancestral gene from which all current copies of the gene are descended), as well as imprints of demographic history on populations and species (Knowles 2009). Among marine zooplankton, mitochondrial markers have been used most regularly to infer demographic history (e.g., Peijnenburg et al. 2005; Aarbakke et al. 2014; Cornils et al. 2017), including marine invasions (Cristescu 2015; Lee 2016; Sherman et al. 2016), population expansions and contractions (Edmands 2001), geographic isolation giving rise to speciation events (Lee 2000; Peijnenburg et al. 2004; Miyamoto et al. 2010), and divergence of genetic lineages following major global climate events (Papadopoulos et al. 2005; Blanco-Bercial et al. 2011b; Milligan et al. 2011).

19.3.2. From population genetics to population genomics

Recent advances in High-Throughput Sequencing (HTS) have created exceptional new opportunities for analysis of population genetic diversity and structure of natural populations. Tens of thousands of genomic Single Nucleotide Polymorphisms (SNPs) can be detected and screened for use as genetic makers of population genetic diversity and structure (Helyar et al. 2011; Reitzel et al. 2013). Such population genomic approaches are being widely used among marine organisms (Bierne et al. 2016), including fishes (Hemmer-Hansen et al. 2014). In addition, HTS is yielding both deep coverage and nucleotide-level resolution in simultaneous or multiplexed analysis of numerous genes (e.g., Bybee et al. 2011). Such population genomic approaches are yielding a new view of population structure and connectivity of marine species, based on statistical discrimination of neutral, selected, and hitchhiker loci (Gagnaire and Gaggiotti 2016).

Over the last three decades, genetic research has showed continuous development and a high turnover of molecular markers, from partial DNA sequencing, restriction fragment length polymorphism (RFLP), random amplified polymorphism detection (RAPD) and amplified fragment length polymorphism (AFLP) to microsatellites, insertion-deletion polymorphism (InDel), and single nucleotide polymorphism (SNP; Schlötterer et al. 2014). Historically, development of markers was difficult and

expensive for non-model organisms. However, the advent of HTS has revolutionized this by allowing the genome-wide markers in any organism and for low cost (Ekblom and Galindo 2011). Although simultaneous discovery and genotyping of genome-wide variation has become feasible for tens of individuals with small genome sizes (< 1GB), the individual sequencing of hundreds of individuals with large genomes remains prohibitively expensive (Narum et al. 2013). In addition, sequencing of the complete genome for all individuals is often unnecessary and inflates the bioinformatics demands (Narum et al. 2013). Therefore, for many studies including population genomics, it is more efficient to sequence a limited number of targeted loci, thus increasing their coverage and chance to detect true polymorphism (Ekblom and Galindo 2011).

A revolutionizing solution to address this situation was the development of genotyping-by-sequencing (GBS) approaches that allow sequencing with high throughput technology of a targeted fraction of the genome via various reduced-representation protocols (see review by Crawford and Oleksiak 2016). These approaches result in discovery and simultaneous genotyping of thousands of SNPs even in species with large genomes and little or no previous genomic information. GBS relies on various reduced-representation protocols to target a genome fraction, but four protocols are currently the most popular: RNA-seq, Ampli-seq, Cap-seq (i.e., capture enrichment), and RAD-seq (Davey and Blaxter 2010; Reitzel et al. 2013). Published reduced representation genomic resources are currently available for several species of marine zooplankton, such as the copepods, *Tigriopus californicus* (Foley et al. 2011), *Calanus finmarchicus* (Smolina 2015), and *Centropages typicus* (Blanco-Bercial and Bucklin 2016); and the euphausiid, *Euphausia superba* (Deagle et al. 2015). The number of studies using reduced representation for population genomics in marine zooplankton may be expected to expand in the near future.

The power of genomic SNPs for resolution of regional- to large-scale population structure of zooplankton has been demonstrated for several key species (see Case Studies, below). A large-scale population genetic analysis using genomic SNPs demonstrated that RAD-seq methods performed poorly

in the copepod, *Calanus finmarchicus*, which has a large and complex genome (Smolina 2015). Subsequent studies of this species using targeted resequencing (e.g., Cap-seq) showed promise for accurate SNP identification and detection of genetic structuring for this species (Choquet et al., unpubl. data). Similarly, a study of the copepod, *Centropages typicus*, by Blanco-Bercial and Bucklin (2016) using 1,000s of genomic SNPs obtained by RAD-seq revealed evidence of population structure, in contrast to an earlier study based on mitochondrial gene sequences (Castellani et al. 2012).

Genomic SNPs that show evidence of selection can provide markers of micro-evolution and local adaptation, including identification of the key genes involved in these phenomena. The use of many thousands of genomic markers will also enable further examination of the significance of small-scale genetic heterogeneity of marine zooplankton, including distinguishing genetic "noise" in large and patchy populations from local adaptation to environmental conditions. Large-scale SNP genotyping studies remain very scarce in zooplankton species, but as more studies based on these approaches are published, it will be important to resolve differing conclusions based on the various technical approaches and genetic markers employed.

19.3.3. Genomic basis of adaptation

Population genomic approaches have provided powerful new tools for detection of impacts of selection and evidence of local adaptation (Stapley et al. 2010). Patterns of variation of genomic markers can be statistically evaluated for non-neutrality and correlation with population dynamic, environmental, and evolutionary conditions and drivers (Gagnaire et al. 2015). Non-neutral markers showing evidence of selection can be used to reveal adaptation of populations to local conditions across a species range (Whitehead 2012), although other evolutionary drivers, including introgression and hitchhiking, can also cause such departures from neutrality for genomic traits (Bierne et al. 2013). Nielsen et al. (2009) concluded that few published studies have convincingly documented that non-neutral traits reflect local adaptation, citing reviews by Hedrick (2006) and Levasseur et al. (2007). Recent advances in statistical analysis of genomic markers are enabling more sensitive and accurate detection of local adaptations

(Gayral et al. 2013; Savolainen et al. 2013; De Wit et al. 2015), although these are much more powerful for species with well-characterized genomes, which allows exome capture and sequencing (Jones and Good 2016).

Patterns of differential gene expression can also provide useful insights into local adaptive responses of marine organisms to environmental conditions. There are a number of such studies of marine zooplankton, including target-gene and whole-transcriptome analyses of differential gene expression patterns associated with stress responses and environmental variability (Lauritano et al. 2012; Schoville et al. 2012; De Pittà et al. 2013; Smolina et al. 2015, 2016; Roncalli et al. 2016; Batta-Lona et al. 2017). The genetic and genomic bases of such gene expression differences have received considerable attention (see review by Romero et al. 2014).

19.3.4. Metagenetics and metabarcoding

The exceptional challenge of species identification in zooplankton assemblages, resulting from both phylogenetic diversity and sibling species swarms, has encouraged the development of genetic approaches for both stand-alone and integrative use with morphological taxonomic methods (Bucklin et al. 2016). Metagenetic and metabarcoding approaches analyze DNA recovered from environmental samples and can reflect the biodiversity of entire pelagic communities (de Vargas et al. 2015), with the advantage of detecting 'hidden diversity' of marine zooplankton (Lindeque et al. 2013). These studies use 'universal' PCR primers to amplify one or more gene regions for high throughput sequencing yielding tens of millions of sequences, which are subsequently resolved into operational taxonomic units (OTUs) that can either be matched to reference databases for identification of taxa or used for various statistical measures of biodiversity (Leray and Knowlton 2016). Metabarcoding studies of marine zooplankton have ranged from analysis of the global ocean (Bik et al. 2012; de Vargas et al. 2015) to studies focused on particular habitats and ecosystems, such as estuaries (Abad et al. 2016), the Red Sea (Pearman and Irigoien 2015), among others. Challenges remain for quantitative analysis of taxa using metabarcoding, although recent studies have shown some correlation between OTU frequency and taxon biomass (Hirai

et al. 2015; Sun et al. 2015).

The continuing development of sequencing technologies may soon allow a full metagenomics approach, where DNA extracted from environmental samples is sequenced and whole genomes are reconstructed from the data. These data will be invaluable resources for diverse population genomic approaches, including analysis of population genetic diversity and structure, detection of loci under selection, and genomic bases of adaptations of zooplankton species to environmental variation. Currently, both technical and bioinformatics challenges limit use of metagenomics to species with small genomes, such as the copepod, *Oithona nana* (Madoui et al. 2017).

19.4. Case studies of marine zooplankton

Population genomic approaches, entailing simultaneous sampling of numerous variable loci within a genome and the inference of locus-specific effects (Black et al. 2001; Luikart et al. 2003), are only very recently being used for analysis of marine zooplankton. Comparison between results from population genetic studies using single-markers (usually mitochondrial or microsatellite DNA) and HTS genomic markers are particularly useful to evaluate the power and precision of population genomic approaches for analysis of genetic structure, connectivity, demographic history, and local adaptation.

Several of the marine zooplankton species analyzed using population genomic approaches belong to the crustacean Subclass Copepoda, which comprises more species than any other zooplankton group, including many that are ecologically important, numerically predominant, and geographically widespread. Genomic analysis of copepods has been a focus of research, although progress has been hampered by the exceptionally large genome sizes of many species (Bron et al. 2011; Wyngaard et al. 2011; Jeffrey 2015).

19.4.1. *Calanus finmarchicus* (Copepoda): The planktonic copepod *Calanus finmarchicus* (Fig. 3) is thought to be the most abundant metazoan in the ocean; the species is ubiquitous in coastal and open ocean cold-temperate regions of the North Atlantic Ocean (Planque et al. 1997); within this area, the species may contribute >70% of total copepod biomass (Head et al. 2003) and occupies a pivotal position in ocean food webs (Falk-Petersen et al. 2007). Population genetic studies using mitochondrial DNA

(e.g., Bucklin et al. 1996) and microsatellites (Provan et al. 2009) have shown high levels of gene flow and little or no significant population genetic structure at any spatial scale. Studies using SNPs in targeted gene regions suggested genetic differentiation among samples from different water masses and ocean basins (Bucklin and Kaartvedt 2000; Unal and Bucklin 2010 Fig. 4). Population genomic analyses of *C. finmarchicus* have been impeded by the large size of its genome (C-value = 6.48 pg; McLaren et al. 1988), typical of crustaceans. Smolina (2015) used a genotyping-by-sequencing approach (ddRADseq; Peterson et al. 2012) to characterize genomic SNPs in pooled samples of *C. finmarchicus* collected across the North Atlantic Ocean. Significant population differentiation was observed among locations, although the allelic nature of the SNP variants in the pooled samples could not be confirmed due to the highly-replicated genome (Smolina 2015). An ongoing study by this group is analyzing genomic SNPs in targeted gene regions to allow confirmation of allelic variation despite genome size (Choquet et al. 2017a). A partial reference transcriptome for the species (Lenz et al. 2014) is allowing evaluation of evidence of local adaptation based on transcriptomic and target gene analysis (e.g., Roncalli et al. 2016).

19.4.2. *Centropages typicus* (Copepoda): Blanco-Bercial and Bucklin (2016) used genomic SNPs detected by 2b-RADseq analysis (Wang et al. 2012) to examine population genetic structure of the copepod *Centropages typicus* (Fig. 5) in the North Atlantic Ocean. Thousands of genomic SNP markers were identified; loci showing evidence of positive selection were removed from analysis (Foll and Gaggiotti 2008). Statistical analysis of molecular variance (Excoffier and Lischer 2010) revealed significant differences between continental shelf populations of the NE and NW Atlantic populations, in contrast with an earlier study by Castellani et al. (2012), which showed no structuring using a mitochondrial COI gene region, but some differentiation of NE and NW Atlantic populations based on a nuclear rRNA internal transcribed spacer (ITS) region. Genotyping-by-sequencing (RADtag sequences) of *C. typicus* yielded 675 loci used by Blanco-Bercial and Bucklin (2016) to test hypotheses of dispersal and directional migration (Beerli 2012). Among five different gene flow models (Fig. 6), the full migration model showed the highest support. These results demonstrate the power of population genomic

approaches to resolve patterns and pathways of dispersal of a high gene flow species in a dynamic and complex current system. Such analyses can also be used to examine the genomic basis of observed local adaptation of this species to environmental variability among regions or along a latitudinal gradient (Carlotti et al. 2007).

19.4.3. *Tigriopus californicus* (Copepoda): The tidepool copepod, *Tigriopus californicus*, shows exceptional levels of small-scale population genetic heterogeneity associated with the habitat structure of the rocky shoreline, based on studies using mitochondrial markers (Rawson et al. 2000; Burton et al. 2007). The species may be considered to be a model species for studies of evolutionary divergence and local adaptation (Raisuddin et al. 2007). The rapid rate of evolutionary divergence of mitochondrial genes is thought to contribute to the potential for local adaptation, but may also cause low hybrid fitness by disrupting gene complexes (Burton et al. 2013). The mitochondrial genome has been sequenced (Barreto et al. 2011; Pereira et al. 2016). A genomic SNP linkage map (Foley et al. 2011) and a partial draft genome (https://i5k.nal.usda.gov/Tigriopus_californicus) serve as useful resources for characterizing population genetic diversity and structure. More recently, the capacity of this species to adapt to local condition and stressors has been explored using population genomic and transcriptomic approaches (Lima and Willett 2017; Pereira et al. 2017).

19.4.4. *Acartia tonsa* (Copepoda): The rapid cladogenesis – and perhaps cryptic speciation – of the estuarine copepod, *Acartia tonsa*, has been extensively studied along the Atlantic coastline of the USA using mtDNA marker genes (Caudill and Bucklin 2004; Chen and Hare 2008, 2011). The species has been intensively studied in laboratory culture, partly as food for aquacultured fish (Jepsen et al. 2017) and partly as a model organism for studies of the genetic basis of local adaptation and micro-evolution (Drillet et al. 2008). Responses to environmental stressors have been examined using genomic and transcriptomic approaches (Nilsson et al. 2014; Petkeviciute et al. 2015; Rahlff et al. 2017).

19.4.5. *Euphausia superba* (Euphausiacea): The Antarctic krill, *Euphausia superba* (Fig. 7), is a keystone species of the Southern Ocean pelagic ecosystem, whose high abundance, markedly patchy

distribution, and swarming behavior have long been a subject of research (Siegel and Watkins 2016). The population genetic consequences of this exceptional life history have been studied over many decades using varied markers, including allozymes, mitochondrial DNA, and microsatellites. Many studies have revealed similar patterns of genetic diversity, whereby variation within locations far outweighs that between locations, with consistent evidence of lack of large-scale population differentiation (see review by Jarman and Deagle 2016). Two studies using mitochondrial markers found evidence of significant small-scale patchiness: Batta-Lona et al. (2011) hypothesized that genetic differences among samples resulted from advective transport from distinct recruitment centers in the Western Antarctic Peninsula region. Zane et al. (1998) found genetic differentiation between samples collected in the Weddell Sea and South Georgia. Although the statistical significance of these findings has been questioned (see Bortolotto et al. 2011), small-scale patchiness – or genetic "noise" – may be a consequence of the life history of this unique species and/or evidence of local adaptation. Evidence of micro-evolution and local adaptation by Antarctic krill has been shown in genetic and functional analysis of target genes, including thioredoxin (Li et al. 2017), clock genes (Jones and Good 2016), heat shock proteins (Papot et al. 2016), and opsins (Biscontin et al. 2016), among others. Population genomic analysis of Antarctic krill was introduced by Deagle et al. (2015), who examined circum-Antarctic genetic diversity and structure using both RADseq and mitochondrial (ND1 and COI) markers. The large and highly-replicated genome of *E. superba* (47.7 GB, Jeffery 2012) prevented discrimination of allelic variation versus that between copies at separate loci (see above), which was addressed by analysis of sequence counts at variable nucleotide sites, rather than the derived genotypes. This study confirmed earlier findings of the large-scale panmixia of Antarctic krill populations (Deagle et al. 2015).

19.4.6. *Meganyctiphanes norvegica* (Euphausiacea): The northern krill *Meganyctiphanes norvegica* (Fig. 8) is abundant throughout the North Atlantic and western Mediterranean Sea. The species exhibits clear genetic differentiation among geographic populations based on various mtDNA markers (see review by Patarnello et al. 2010). Consistent evidence of local adaptation of the species, including

enzyme activities (Saborowski and Buchholz 2002), is now being analyzed using differential gene expression made possible by a reference transcriptome (Maas and Blanco-Bercial 2016).

19.4.7. *Pleurobrachia bachei* (Ctenophora): A draft genome of the ctenophore *Pleurobrachia bachei* (Fig. 9) revealed the possible preservation of 'ancient molecular toolkits' (Moroz et al. 2014), which are lost in other lineages. The exceptional nature of the genomic architecture of this species can provide new understanding of the genomic basis of their evolutionary success and potential for adaptation. Integrative and comparative analysis of genomic and transcriptomic data of this and another ctenophore species *Mnemiopsis leidyi* demonstrated the phylogenetic position of the phylum as the first metazoan lineage (Ryan et al. 2013; Moroz et al. 2014).

19.4.8. *Spadella cephaloptera* (Chaetognatha): Arrow worms are predatory zooplankton that occupy key positions in pelagic food webs. The phylum comprises many species with cosmopolitan-but-disjunct biogeographical distributions, which has allowed interesting comparisons among species. Population genetic diversity and structure of several chaetognath species have been explored using both mtDNA and microsatellites (Peijnenburg et al. 2004, 2006; Faure and Casanova 2006; Miyamoto et al. 2010; Kulagin et al. 2014). Large-scale studies have also allowed examination of the demographic histories of the species (Peijnenburg et al. 2005). Analysis of the mitochondrial genome of *Spadella cephaloptera* (Fig. 10) yielded evidence of exceptional intraspecific variation (Marlétaz et al. 2017), and resolved the phylogenetic position of the Chaetognatha within Protostome lineages (Papillon et al. 2004).

19.4.9. *Salpa thompsoni* (Tunicata, Thaliacea): The Southern Ocean salp *Salpa thompsoni* (Fig. 11) is a pivotal species in the pelagic ecosystem of Antarctic regions, including the Western Antarctic Peninsula, one of the fastest warming regions of the world oceans. A reference transcriptome for *S. thompsoni* is available, although only 18% of the 216,931 sequences were associated with predicted, hypothetical, or known proteins (Batta-Lona et al. 2017). Another recent study (Jue et al. 2016) produced a preliminary reference genome for the species, identified more than 50% of sequences, and generated both SNP variant and INDEL predictions as a resource for future phylogenetic and population studies.

The genome of this species shows evidence of a rapid evolutionary rate – consistent with other Urochordata (Denoeud et al. 2010; Tsagkogeorga et al. 2012). An initial survey of small RNAs revealed the presence of known, conserved miRNAs, novel miRNA genes, and unique piRNA for various developmental stages (Jue et al. 2016), suggesting possible genomic bases of the successful adaptation of the species to the changing climate of the Southern Ocean.

19.5. Present-day challenges and future opportunities

19.5.1. Additional genomic resources for marine zooplankton species

Pelagic zones represent one of the largest (by volume) habitats on Earth, with highly diverse and ecologically important assemblages of zooplankton, which can serve as early warning indicators of climate change. Genomic resources are needed to facilitate both intra- and interspecies comparative studies of genetic diversity and structure, phylogeography, demographic history, and adaptive evolution. Importantly, marine zooplankton provide a diverse and useful assemblage to move forward novel studies of the genomic basis of adaptation and evolutionary divergence. Yet the exceptional phylogenetic diversity of marine zooplankton exacerbates the challenges of ensuring that reference genomes are available for abundant and ecologically-important species or their close relatives.

Whole-genome sequencing initiatives should cover a wide range of genome sizes to uncover trends in genome evolution and new elements of genome organization. For instance, sequencing of the salp genome revealed novel miRNA genes and unique piRNAs (Jue et al. 2016), while the genome of Pacific sea gooseberry, *Pleurobrachia bachei*, is apparently lacking the canonical miRNA machinery and HOX genes (Moroz et al. 2014).

Stimulating discoveries are anticipated from sequencing the exceptionally large genomes of many crustaceans, including euphausiids, copepods, and amphipods, which may reveal novel regulation of repetitive elements, functional divergence of gene duplication and concomitant novel functions of various gene copies, and correlation between genome size and DNA methylation levels in metazoans (e.g., Lechner et al. 2013). From a practical perspective, even low-coverage genomes will increase the

robustness of population genomic approaches by facilitating a diverse range of methods, including in-silico digestion of genome sequences for RAD-seq techniques, higher mapping rates for DNA and RNA-derived sequences, and the development of baits for sequence capture experiments.

Despite their ecological importance in pelagic food webs and their phylogenetic diversity, marine zooplankton have been – and continue to be – largely ignored in the prioritization of species for genomic and transcriptomic analysis. For example, a list of top priority species for reference genome determination from Voolstra et al. (2017) includes only one marine zooplankton species, the mid-water shrimp, *Acanthephyra purpurea*.

19.5.2. Sampling zooplankton in the global ocean

Sampling zooplankton accurately and effectively is a challenge due both to the nature of the pelagic habitat and the frequently immense population sizes of the organisms compared to sampling capacity. It is essential to keep in mind that planktonic organisms most usually occur in patchy distributions, and that some of them are able to avoid the sampling equipment. The origin of these planktonic assemblages or patches has been discussed over many years (e.g., Levin and Segel 1976) and some experimental studies have shown species-specific patterns (Omori and Hamner 1982). Avoidance behaviors also vary among species, and a number of studies have shown that net size and design can markedly impact avoidance and improve the accuracy of sampling of dense and diverse assemblages (Wiebe 1968; Skjoldal et al. 2013; Wiebe et al. 2013). Novel instrumentation designs are now allowing pairing of net sampling with optical and acoustical technologies to allow adaptive sampling of target species of particular interest and importance.

19.5.3. Species identification

Accurate and precise identification of species is critical for any study, yet for most zooplankton groups this goal is challenging – at best. Morphological identification has been shown to be unreliable for numerous species, including sibling species of the copepods *Pseudocalanus* (Bailey et al. 2015) and *Calanus* (Choquet et al. 2017b). Both transcriptomic and genomic resources are invaluable in allowing

the design of rapid and inexpensive protocols for accurate discrimination and identification of sibling and cryptic species of marine zooplankton (e.g., Smolina et al. 2015).

19.5.4. Genomic analysis of small-sized organisms

Zooplankton species are often very small and thus the yield of DNA extractions is limited. This is not an issue for current HTS methods, which usually require a very small amount of DNA (10s ng). The ongoing development of new sequencing platforms and technologies will likely allow longer sequencing reads and thus better genome and transcriptome assemblies. There is a continuing need to ensure that even the tiniest organisms will be amenable to any new developments in sequencing technologies and instrumentation.

19.5.5. Genomic basis of adaptation

Marine environments are experiencing rapid changes in critically-important processes and parameters, including temperature, light penetration, nutrient availability and ocean acidification, among many others. The resultant changes in species physiological condition, ecological functioning, and biogeographical distribution and abundance will inexorably alter pelagic ecosystems in trajectories that are difficult to predict. How species may acclimate and/or adapt to environmental change, and how their interactions within the pelagic food web may be altered, can be examined at many levels. A powerful and important approach lies in examining the underlying genomic mechanisms that facilitate successful adaptation to changing environmental conditions. Although any given species may be uniquely impacted by the physical and biological parameters accompanying shifts in global climate profiles, processes involved in responses to climate change at the molecular level may share common features across species, such as the evolution of gene networks associated with environmental stress responses. Genomic resources are proving instrumental in garnering new insights into organism – environment interactions, including responses to environmental variability associated with climate change. However, we still lack a fundamental understanding of genomic features that afford plasticity and facilitate adaptive responses. These challenges can only be met with comprehensive genomic and transcriptomic resources that will

afford comparative analysis to investigate the mechanisms underlying the responses of marine zooplankton to the changing environmental conditions throughout the global ocean.

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19.7. Table Legends and Tables

Table 1. Holozooplankton species for which genome assemblies and accompanying statistics are publicly available (as of June 2017). Estimated genome sizes are based on assembly statistics unless otherwise noted.

	Tunicates			Ctenophores		Copepods			
	Oikopleura dioica	*Oikopleura dioica*	*Salpa thompsoni*	*Pleurobrachia bachei*	*Mnemiopsis leidyi*	*Eurytemora affinis*	*Oithona nana*	*Tigriopus kingsejongensi*	*Tigriopus californicus*
	Main assem	Allelic assem							
Assembly Name	ASM20953v1	ASM20955v1	Salp Genome 1.0	P.bachei_draft_genome_v.1.1	GCA_000226015.1	Eaff_1.0	O. nana v.1.0	NA	TCALIF_v1.0
Estimated Genome Size (MB)	68.46	allelic assembly	602[a]	170	150	616.14[b]	85	298	245[d]
Assembly Size	70,471,451	45,141,193	318,747,957	156,121,975	155,865,547	494,890,867	85,010,107	305,712,242	184,634,130
Predicted protein coding Genes	18,020	18,020	13,186	19,523	16,548	29,783	15,359	12,772	14,536
Coverage	14X	N/A[c]	20X	200X	160X	75X	N/A[c]	65X	N/A[c]
Number of scaffolds	1,260	4,196	478,281	21,979	5,100	6,899	4,626	27,823	2,365
Length of N50 scaffold (bp)	395,387	21,890	934	20,628	187,314	862,645	400,614	159,218	298,012
Number of N50 scaffold (L50)	35	478	79,492	1,646	242	163	60	N/A[c]	180
Number of contigs	5,917	6,678	590,021	38,864	24,884	122,625	7,437	48,368	26,175
Length of N50 contig (bp)	24,932	10,847	636	6,132	11,936	5,738	38,620	17,566	14,799
Number of N50 contig	718	985	136,534	6,078	3,653	19,338	463	N/A[c]	3,352
Length of gaps (bp)	3,938,358	2,655,217	14,945,692	19,276,734	5,525,119	107,316,113	2,943,785	10,474,460	N/A[c]
References	Denoeud et al. (2010)	Denoeud et al. (2010)	Jue et al. (2016)	Moroz et al. (2014)	Ryan et al. (2013)	Eyun et al. (2017)	Madoui et al. (2017)	Kang et al. (2017)	https://i5k.nal.usda.gov/Tigriopus_californicus

[a] genome size estimate independent of assembly (Jue et al. 2016)

[b] genome size estimate independent of assembly (Rasch et al. 2004)

[c] not available/not provided

[d] genome size estimate independent of assembly (Wyngaard and Rasch 2000)

Table 2: Mitochondrial genomes available for marine zooplankton species, with corresponding lengths.

Taxon and Species	Citation	Length (bp)
Copepoda		
Calanus hyperboreus	Kim et al. (2013)	17,910
Calanus sinicus	Minxiao et al. (2011)	>20,460
Paracyclopina nana	Ki et al. (2009)	15,981
Tigriopus californicus	Burton et al. (2007)	14,600
Tigriopus japonicus	Machida et al. (2002)	14,628
Tigriopus sp.	Jung et al. (2006)	14,301
Euphausiacea		
Euphausia pacifica	Shen et al. (2011)	16,898
Euphausia superba	Shen et al. (2010)	>15,498
Ostracoda		
Vargula hilgendorfii	Ogoh & Ohmiya (2004)	15,923
Amphipoda		
Onisimus nanseni	Ki et al. (2010)	14,734
Decapoda		
Acetes chinensis	Kim et al. (2012)	15,740
Cnidaria		
Aurelia aurita	Shao et al. (2006)	16,937
Cassiopea frondosa	Kayal et al. (2011)	15,949
Chrysaora quinquecirrha	Hwang et al. (2014)	16,775
Ctenophora		
Mnemiopsis leidyi	Pett et al. (2011)	10,000
Pleurobrachia bachei	Kohn et al. (2012)	11,016
Chaetognatha		
Sagitta decipiens	Miyamoto et al. (2010)	11,121
Sagitta enflata	Miyamoto et al. (2010)	12,631
Sagitta ferox	Li et al. (2016)	12,153
Sagitta nagae	Miyamoto et al. (2010)	11,459
Paraspadella gotoi	Helfenbein et al. (2004)	11,423
Pterosagitta draco	Wei et al. (2016)	10,426
Spadella cephaloptera	Papillon et al. (2004)	11,905

Table 3. Summary of transcriptomic resources for marine zooplankton species. Transcript and gene numbers are indicated as presented in the original study. Note that different methodologies were employed across these datasets (e.g. Trinity, MIRA_Newbler, Evigene, FPKM filtered, etc) that render cross-comparisons of gene and transcript numbers among species equivocal.

Phylum and Species	BioProject	Contig Total	Contig Max Length	Contigs Total Length	Contigs Annotated	Transcripts	N50	Genes	Citation
Cnidaria									
Alatina alata	PRJNA312373	31,737	32,591	48,508,802	No	31,776	2,545	20,173	Ames et al. (2016)
Rhopilema esculentum	PRJNA318143	148,857	30,742	121,470,903	No	NA	NA	NA	Chongbo and Yunfeng (Dir Sub)
Aurelia aurita	PRJNA252562	252,170	46,960	180,188,094	No	24,264	1,761	10,285	Brekham et al. (2015)
Ctenophora									
Mnemiopsis leidyi	PRJNA344880	140,842	29,348	137,638,938	No	NA	NA	NA	Sanchez Alvarado, Gotting and Ross (Dir Sub)
Arthropoda: Copepoda									
Acartia fossae		100,383	8,174		No		769		Eyun et al. (2017)
Calanus finmarchicus	PRJNA236983	28,954	2,945	10,223,122	No	251,042	354	13,057	Smolina et al. (2014)
Calanus finmarchicus	PRJNA236528	206,012	23,068	205,455,659	Yes		1,418		Lenz et al. (2014)
Calanus finmarchicus	PRJNA231164	241,140	25,048	160,760,719	No				Tarrant et al. (2014)
Calanus glacialis	PRJNA237014	36,880	4,021	15,748,490	No	242,602	471	18,387	Smolina et al. (2014)
Calanus glacialis	PRJNA274584	54,344	7,507	33,214,362	No	16,998	620	16,998	Ramos et al. (2015)
Calanus sinicus		69,751				69,751	1,127	43,417	Yang et al. (2014)
Calanus sinicus			3,923		No	29,458	513		Eyun et al. (2017)
Eucyclops serrulatus	PRJNA231234	51,528	16,342	36,645,141	No				Cattonaro (Dir Sub)
Eurytemora affinis	PRJNA278152	107,445	26,685	142,143,154	No	29,783			Monroe (Dir Sub)
Eurytemora affinis	PRJNA242763	138,088	23,627	143,733,589	Yes				Almada and Tarrant (Dir Sub)
Eurytemora affinis		88,104	26,685						Eyun et al. (2017)
Paracyclopina nana	PRJNA268783	60,687	27,858	95,849,484	Yes	67,179	4,178	12,474	Lee et al. (2015)
Pseudocalanus acuspes	PRJNA296544	207,302	12,713	59,236,626	Yes	69,555	1,348	28,879	De Wit et al. (2016)
Tigriopus kingsejongensis	PRJNA283925	38,250	7,809	36,497,199	Yes				Lee (Dir Sub)
Tigriopus kingsejongensis			23,942	28,850,726		40,172	1,093	12,772	Kang et al. (2017)
Tigriopus californicus	PRJNA263967	12,067	13,452	14,966,851	No				Barreto et al. (2011)
Tigriopus californicus	PRJNA263967	12,075	13,452	14,902,878	No				Barreto et al. (2011)
Tigriopus californicus		106,317	27,644	NA	Yes	106,317	2,837	12,573	Periera et al. (2016)
Tigriopus californicus		60,840	8,614				1,510		Eyun et al. (2017)
Tigriopus japonicus	PRJNA274317	54,758	23,769	82,981,758	Yes		3,565		Kim et al. (2015)
Arthropoda: Euphausiacea									
Euphausia superba			11,127		Yes	15,347	520	7,942	Meyer et al. (2015)
Euphausia superba		22,177	8,515		Yes			5,563	Clark et al. (2011)
Euphausia superba		133,962		129,183,922	Yes		1,294	27,928	Sales et al (2017)
Euphasia crystallorophias		42,632					8,341		Toullec et al. (2013)
Meganyctiphanes norvegica	PRJNA324094	405,497	26,644	222,530,071	No	NA	NA	NA	Maas and Blanco Bercial (Dir Sub)
Arthropoda: Amphipoda									
Talitrus saltator	PRJNA297565	156,706	22,032	151,674,147	Yes		968		O'Grady et al. (2016)
Arthropoda: Mysidacea									
Neomysis awatschensis	PRJNA287057	22,141	10,398	14,999,154	Yes	22,141	801		Kim et al. (2016)
Mollusca: Pteropoda									
Clio pyramidata	PRJNA231010	45,735				45,735	852	30,800	Maas et al. (2015)
Clione limacina	PRJNA314884	477,401	30,190	258,267,445	Yes	300,994	816	181,879	Thabet et al. (2017)
Limacina antarctica	PRJNA295792	81,226	7,935	59791880	No	402,273	500	81,229	Johnson and Hoffman (2016)
Limacina helicina	PRJNA386290	53,121	12,358	31,790,000	Yes		796		Koh et al. (2015)
Urochordata: Tunicata									
Oikopleura dioica	PRJNA269316	54,949	23,096	66,526,340	No				Wang et al. (2015)
Oikopleura dioica	PRJNA269317	86,898		70,800,000		57,962	1,806	16,423	Wang et al. (2015)
Salpa thompsoni	PRJNA279245	217,849	30,785	151,741,986	No	216,931	1,163	26,413	Jue et al. (2016); Batta Lona et al. (2017)

19.8. Figure Legends

Figure 1. Distribution of estimated genome sizes in representative holozooplankton phyla. Black dots indicate sequenced genomes. Genome size estimations are from Gregory (2017), Jeffery et al. (2017), Leinaas et al. (2016), Ryan et al. (2014), Moroz et al. (2014), and Madoui et al. (2017).

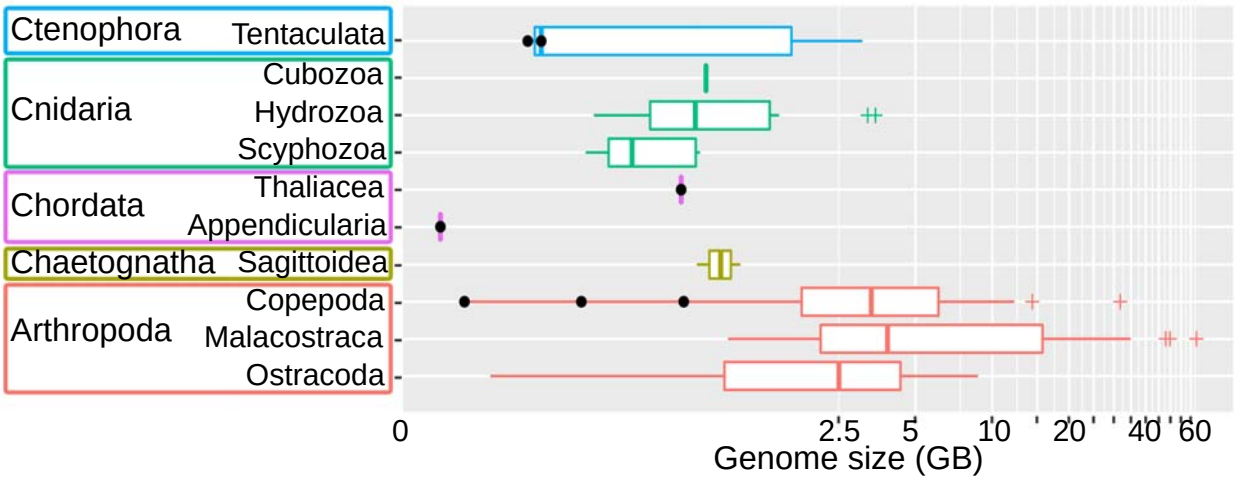


Figure 2: Comparison of the mitochondrial gene order between *Calanus sinicus* and *C. hyperboreus*. Only the 13 protein-coding genes are represented. Rectilinear shapes show genes for which the order is conserved between the two species; red lines indicate genes with the same sequence but in reverse order between the species.

Figure 3. *Calanus finmarchicus* (Copepod) http://umaine.edu/jrunge/files/2013/12/CV_1_for-publication.jpg (Photo J.R. Runge, University of Maine)

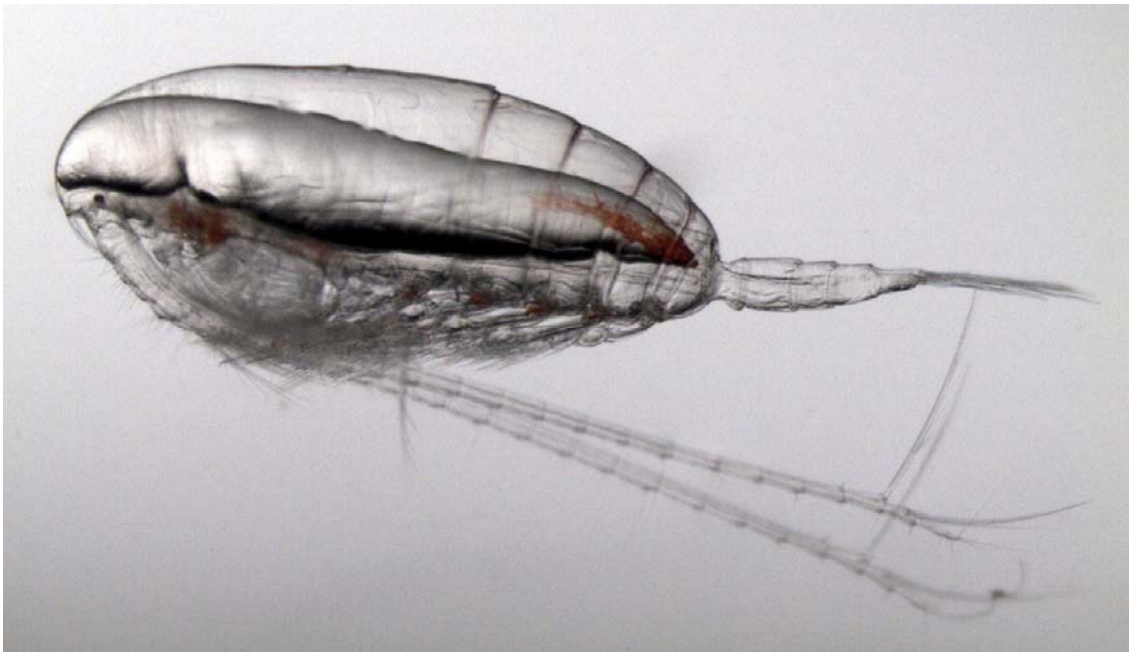


Figure 4. Circulation patterns and bathymetry of the North Atlantic Ocean basin, providing the foundation of the three-gyre hypothesis for basin-scale dispersal of the copepod *Calanus finmarchicus*. Figure from Wiebe et al. (2009).

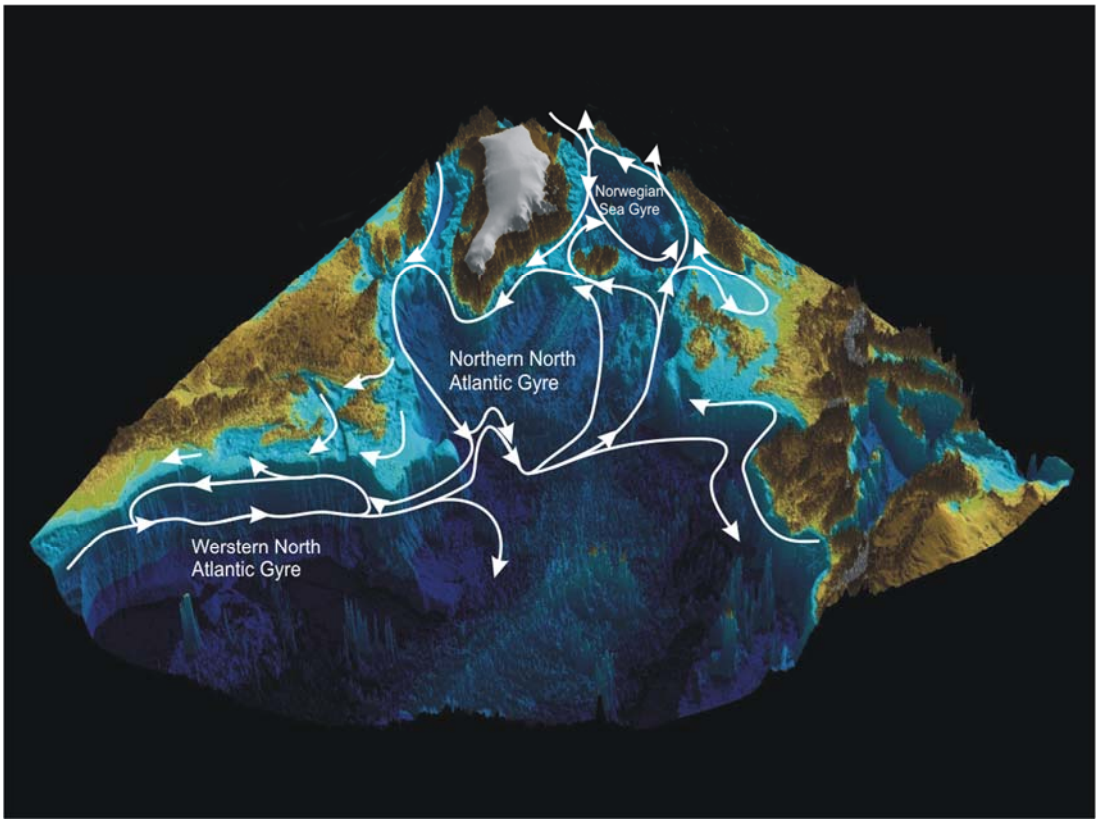


Figure 5. *Centropages typicus* (Copepod) https://alchetron.com/Centropages-2143715-W (Photo Slotwinski, University of Tasmania)

Figure 6. Hypothesized models of gene flow and population connectivity of the copepod *Centropages typicus*. The full migration model (lower right in diagram) showed the highest likelihood among the considered models based on Bayesian analysis. Figure from Blanco-Bercial and Bucklin (2016).

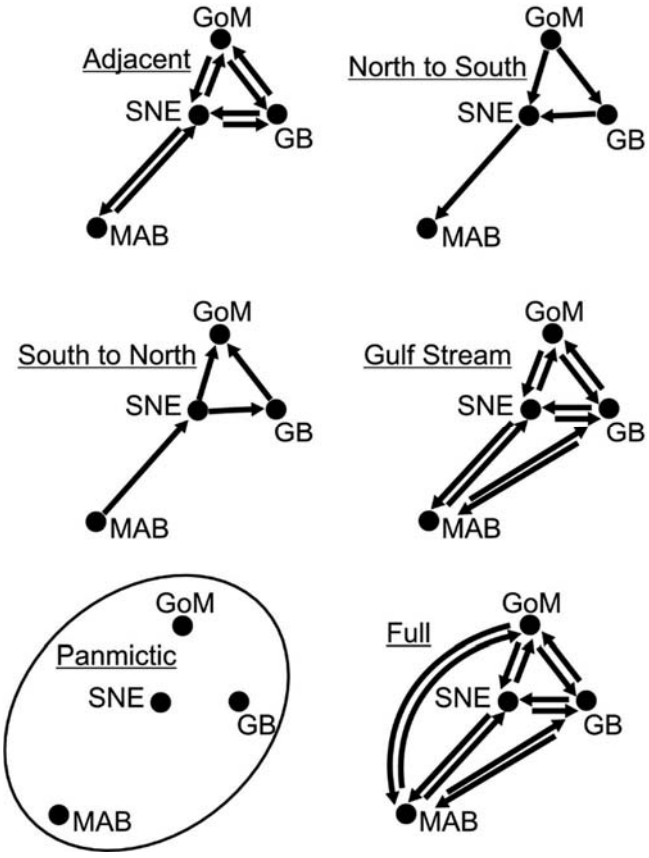


Figure 7. *Euphausia superba* (Euphausiid) http://www.ecoscope.com/krill/krill4/index.htm (Photo Uwe Kils, Rutgers University, USA)

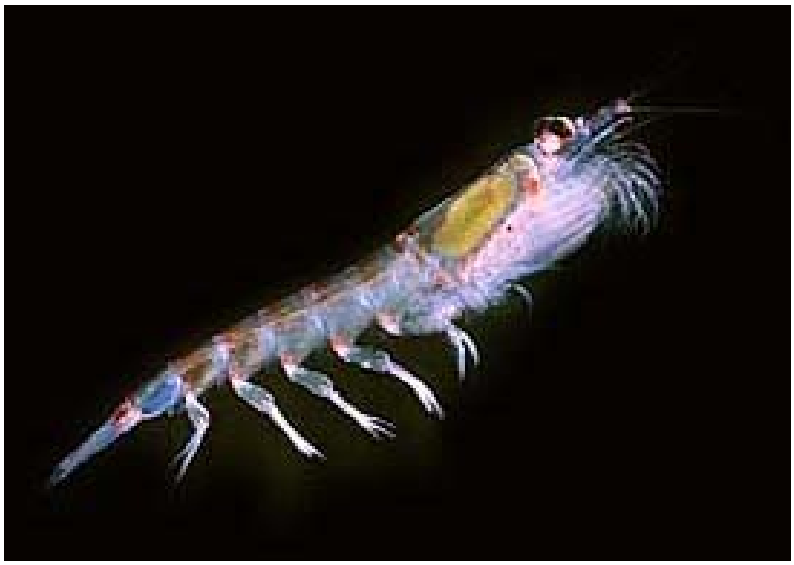


Figure 8. *Meganyctiphanes norvegica* (Euphausiid)

https://en.wikipedia.org/wiki/Northern_krill#/media/File:Meganyctiphanes_norvegica.jpg (Photo Uwe Kils, Rutgers University, USA)

Figure 9. *Pleurobrachia bachei* (Ctenophora) http://jellieszone.com/ctenophores/pleurobrachia/ (Photo Dave Wrobel)

Figure 10. *Spadella cephaloptera* (Chaetognatha) http://australianmuseum.net.au/image/Arrow-worm-Chaetognaths (Photo Peter Parks, Image Quest 3-D)

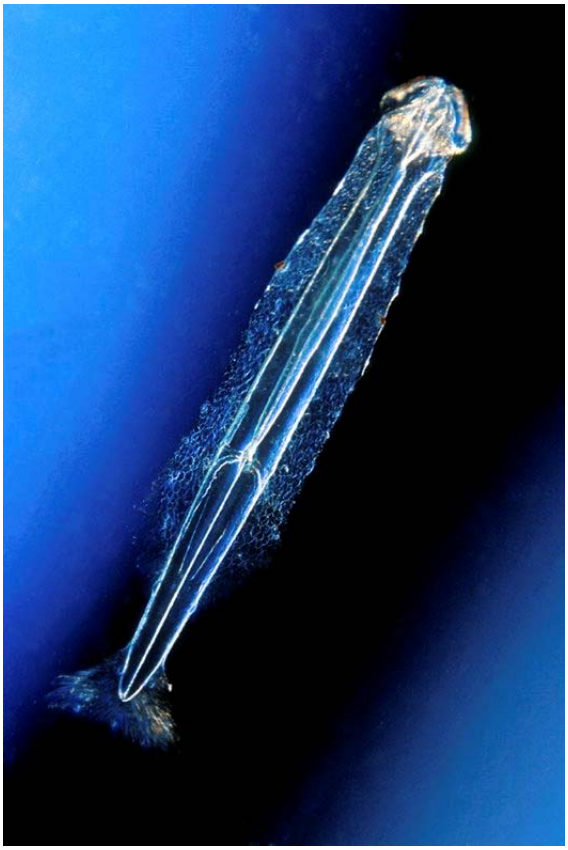
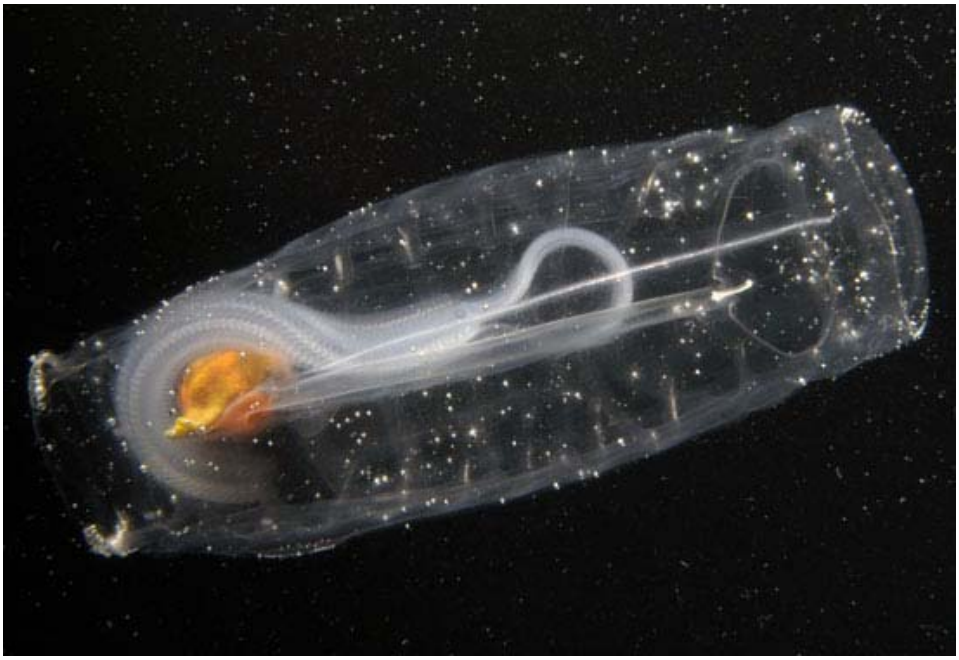


Figure 11. *Salpa thompsoni* (Tunicata, Thaliacea)

http://www.whoi.edu/cms/images/oceanus/2005/6/v44n1-briefs2-3en_10823.jpg (Photo L.P. Madin, Woods Hole Oceanographic Institution)



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