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High evolutionary potential of marine zooplankton

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Abstract

Open ocean zooplankton often have been viewed as slowly evolving species that have limited capacity to respond adaptively to changing ocean conditions. Hence, attention has focused on the ecological responses of zooplankton to current global change, including range shifts and changing phenology. Here, we argue that zooplankton also are well poised for *evolutionary responses* to global change. We present theoretical arguments that suggest plankton species may respond rapidly to selection on mildly beneficial mutations due to exceptionally large population size, and consider the circumstantial evidence that supports our inference that selection may be particularly important for these species. We also review all primary population genetic studies of open ocean zooplankton and show that genetic isolation can be achieved at the scale of gyre systems in open ocean habitats (100s to 1000s of km). Furthermore, population genetic structure often varies across planktonic taxa, and appears to be linked to the particular ecological requirements of the organism. In combination, these characteristics should facilitate adaptive evolution to distinct oceanographic habitats in the plankton. We conclude that marine zooplankton may be capable of rapid evolutionary as well as ecological responses to changing ocean conditions, and discuss the implications of this view. We further suggest two priority areas for future research to test our hypothesis of high evolutionary potential in open ocean zooplankton, which will require (1) assessing how pervasive selection is in driving population divergence and (2) rigorously quantifying the spatial and temporal scales of population differentiation in the open ocean.

Evolution in the Open Sea

The oceans are changing on a global scale and, in some cases, at rates greatly exceeding those observed in the historical and recent geological record (e.g., Pelejero et al. 2010). Holoplankton, the organisms that spend their entire life cycle in the open water column, are particularly good indicators of climate change (Hays et al. 2005), and show the most dramatic range shifts of any organisms reported in either terrestrial or marine environments (e.g., Beaugrand et al. 2002, 2009; Burrows et al. 2011). Marine zooplankton serve as key links in the food web between primary producers and higher trophic levels (e.g., fish, micronekton), and also are important mediators of biogeochemical fluxes in the ocean. Marine zooplankton are a phylogenetically diverse group (see Fig. 1) including representatives from 12 animal phyla (Angel 1993). Most taxa are diploid and sexual species, but some notable exceptions include members of the phyla Cnidaria and Urochordata, which alternate between asexual and sexual phases of their life cycle (e.g., scyphozoans, salps).

Although we know very little about the evolutionary potential of open ocean zooplankton, most authors have explicitly or implicitly assumed that zooplankton will show limited evolutionary responses to climate change (e.g., Helaouët and Beaugrand 2009; Reygondeau and Beaugrand 2010; Stegert et al. 2010; but see Dam 2013). Hence, much attention has been focused on the observations of ecological responses to climate change in these species, for example, on their changing species' distributions and phenology (e.g., Hays et al. 2005; Richardson

Figure 1. Examples of the diverse holozooplankton assemblage of the Atlantic ocean (members of the phyla Arthropoda, Mollusca, Annelida, Cnidaria, and Chaetognatha are represented). Photographed by the authors during the Atlantic Meridional Transect (AMT22) research cruise in October–November 2012.

2008; Ji et al. 2010). Here, we consider evolutionary responses, that is, those that result in genetic changes in a population, for example, in response to selective pressure. Although the number of studies that have rigorously tested for genetic adaptation in marine zooplankton is small, and limited to estuarine and coastal taxa that are amenable to laboratory experimentation (reviewed in Dam 2013), unequivocal evidence exists for genetic adaptation in marine zooplankton. One example is that grazer populations with a history of exposure to toxic algal blooms have significantly higher fitness when challenged with toxic prey than those with little or no such history of exposure (Colin and Dam 2007). There is also an extensive literature providing evidence for adaptive evolution in freshwater zooplankton, for example, using the water flea *Daphnia* as a model system (e.g., Critescu et al. 2012; Orsini et al. 2012). Our review focuses on the open ocean zooplankton, the majority of which cannot be cultured in the laboratory. We argue that evolutionary responses to global change are important to consider for these taxa, and explore indirect methods for studying evolution in these oceanic species.

Three primary arguments have traditionally supported the perception that open ocean zooplankton have limited capacity to evolve in comparison to other terrestrial and marine species (e.g., van der Spoel and Pierrot-Bults 1979; Angel 1992; Palumbi 1992; Grosberg and Cunningham 2001). First, low species diversity in the plankton has been interpreted as evidence for depressed speciation rates in comparison to other organisms. The pelagic habitat lacks obvious geographic isolating barriers that would be necessary for speciation in allopatry, the most common geographic mode of speciation (Pierrot-Bults and van der Spoel 1979; Angel 1993; van der Spoel 1994; Norris 2000; Coyne and Orr 2004). Although molecular studies are revealing cryptic species across the spectrum of pelagic animal phyla (Dawson and Jacobs 2001; Darling and Wade 2008; Morard et al. 2009; Goetze 2010a; Jennings et al. 2010; Miyamoto et al. 2010; Ortman et al. 2010), true estimates of species numbers are unlikely to be orders of magnitude higher than current estimates. A recent estimate of global marine diversity reported that ~226,000 eukaryotic marine species are described, of a total of 0.7–1.0 million marine species (Appeltans et al. 2012). Of these, only a small fraction are DNA barcoded (Bucklin et al. 2011), and molecular methods are estimated to add tens of thousands, rather than hundreds of thousands, of species to the currently accepted species list (Appeltans et al. 2012). Thus, we can accept that species diversity in the plankton is relatively low. Second, marine zooplankton have among the largest (effective) population sizes of any organisms on Earth (e.g., Lynch et al. 1991; Bucklin and Wiebe 1998; Avise 2000; Goetze 2005; Peijnenburg et al. 2005), and therefore genetic drift is expected to be ineffective at changing allele frequencies within these populations. Third and finally, marine plankton are envisioned to be high-dispersal species (Ekman 1953; Angel 1993; van der Spoel 1994), with extensive migration among populations limiting their capacity for local adaptation. Plankton have been likened to airborne spores or wind-dispersed seeds that can drift almost anywhere in the ocean (Norris 2000), with their biogeographic ranges limited only by their ability to find suitable habitat for the establishment of new populations (Norris and de Vargas 2000; Sexton and Norris 2008). Collectively, these three arguments have supported a persistent view of low evolutionary potential for marine zooplankton, in comparison to other marine and terrestrial groups. However, a number of recent observations and insights suggest that we may have overlooked important processes driving the evolution of open ocean zooplankton. Here, we propose the idea that selection may be a dominant driver of marine zooplankton evolution based on theoretical insights and circumstantial evidence that selection may be widespread in these species. We also review the 46 primary population genetic and phylogeographic studies that focus on population-level differentiation in marine zooplankton (55 taxa; Table 1), and show that

Table 1. Summary of all 46 population genetic and phylogeographic studies that focus on open ocean zooplankton.

Species name	Geographic area	Marker type	Sample size	Presence and scale of structure	Pairwise F_{ST} (range)	h	pi	Dev. neutr.?	Reference
Planktonic copepods									
Labidocera aestiva	W. North Atlantic, US coast	Allozymes (6 loci)	211	Regional, within NW Atlantic	n.r.	N/A	N/A	N/A	Bucklin and Marcus (1985)
Calanus australis	Tropical and subtropical Pacific	Allozymes (2 loci)	328	Panmixia, but high variation in this species	n.r.	N/A	N/A	N/A	Afanas'yev et al. (1989)
Undinula darwinii	Tropical and subtropical Pacific	Allozymes (2 loci)	742	Isolation by distance observed (over 3000 km)	n.r.	N/A	N/A	N/A	Afanas'yev et al. (1989)
Metridia pacifica	California Current	Allozymes (7 polymorphic loci)	n.r., >420	Genetic heterogenity, weak or absent structure	0.011–0.141	N/A	N/A	N/A	Bucklin et al. (1989)
Metridia pacifica	California Current	Allozymes (6 loci)	3040	Genetic heterogenity, some structure at mesoscale	n.r.	N/A	N/A	N/A	Bucklin (1991)
Calanus finmarchicus	W. North Atlantic	mtDNA sequence (16S rRNA)	182^1	Genetic heterogenity, but not structured	n.r.	n.r.	0.0042	n.r.	Bucklin and Kocher (1996)
Calanus finmarchicus	Gulf of Maine	Allozymes, mtDNA RFLPs	628	Panmixia	0.021–0.039	N/A	n.r.	N/A	Kann and Wishner (1996)
Calanus finmarchicus	W. North Atlantic and Norwegian Sea	mtDNA sequence (16S rRNA)	104^1	Weak structure between NW Atlantic and Norwegian Sea	n.r.	0.670	0.0061	n.r.	Bucklin et al. (1996a)
Nannocalanus minor	NW and NE Atlantic	mtDNA sequence (16S rRNA)	155^1	Panmixia within Types I and II	n.r.	0.880	0.0232	n.r.	Bucklin et al. (1996b)
Nannocalanus minor	W. subtropical North Atlantic	mtDNA sequence (16S rRNA)	158	n.r.	n.r.	0.824	0.0050	n.r.	Bucklin and Wiebe (1998)
Calanus finmarchicus	Boreal North Atlantic	mtDNA sequence (16S rRNA)	216	n.r.	n.r.	0.368	0.0037	n.r.	Bucklin and Wiebe (1998)
Calanus finmarchicus	Boreal North Atlantic	Nuclear SNPs (2 loci)+ and DNA sequence	92^1	Regional, among Iceland samples	n.r.	n.r.	n.r.	n.r.	Bucklin et al. (2000a)
Acartia clausi	Five Norwegian fjords (NE Atlantic)	mtDNA sequence (16S rRNA)	96	Between Norwegian Fjords	n.r.	0.674	0.0026	n.r.	Bucklin et al. (2000b)
Calanus helgolandicus, C. euxinus	NE Atlantic, Mediterranean, Black Sea	mtDNA sequence (COI, cyt b)	72^1	Between basins	0.000–0.524	0.703	0.0028	Yes	Papadopoulos et al. (2005)
Eucalanus spinifer	Global	mtDNA sequence (COI)	383^1	Between basins and central gyres	0.000–0.587	0.487	0.0022	Yes	Goetze (2005)

(*Continued*)

Table 1. Continued.

Species name	Geographic area	Marker type	Sample size	Presence and scale of structure	Pairwise F_{ST} (range)	h	pi	Dev. neutr.?	Reference
Eucalanus hyalinus	Global	mtDNA sequence (COI)	450	Between basins and central gyres	0.000–0.826	0.887	0.0276	Yes	Goetze (2005)
Calanus helgolandicus, C. euxinus	NE Atlantic, Mediterranean, Black Sea	mtDNA sequence (COI)	99^1	Regional, between basins, European Seas	0.316–0.509	0.860	n.r.	n.r.	Unal et al. (2006)
Macrosetella gracilis	North Pacific, North Atlantic	mtDNA sequence (COI)	149^1	Within and between basins	0.117–0.235	0.899	0.0168	No	Eberl et al. (2007)
Calanus pacificus	Boreal North Pacific	mtDNA sequence (COI)	398	Between coastal and open ocean sites	0.060–0.750	0.912	0.0089	n.r.	Nuwer et al. (2008)
Calanus finmarchicus	Boreal North Atlantic	mtDNA sequence, Microsats	313	Panmixia	n.r.	n.r.	n.r.	n.r.	Provan et al. (2009)
Calanus glacialis	N Atlantic, Arctic, N Pacific	mtDNA sequence (16S rRNA)	443^1	Strong structure between Pacific and Arctic Ocean	0.000–0.680	0.295	n.r.	n.r.	Nelson et al. (2009)
Disseta palumbii	equatorial W Pacific, marginal seas	AFLPs	34^1	Between Sulu Sea vs other regions (clade B)	0.000–0.018	0.236	0.0208	n.r.	Machida and Nishida (2010)
Calanus finmarchicus	Boreal North Atlantic	Nuclear SNPs (3 loci)	351^1	Weak structure, within and between regions	0.000–0.240	n.r.	n.r.	n.r.	Unal and Bucklin (2010)
Subeucalanus pileatus	Global	mtDNA sequence (16S rRNA)	204	Within and between basins	0.000–0.997	0.439	0.0023	n.r.	Goetze (2010b)
Clausocalanus lividus	North Pacific, North Atlantic	mtDNA sequence (COI)	87^1	Clade divergence, between basins	0.000–1.000	0.874	0.0337	No	Blanco-Bercial et al. (2011)
Clausocalanus arcuicornis	Global	mtDNA sequence (COI)	96^1	Within and between basins	0.0618–0.301	0.958	0.0180	Yes	Blanco-Bercial et al. (2011)
Acartia tonsa – lineage X	W. North Atlantic, US coast	mtDNA (COI) and nucDNA (ITS1) sequence	88	Little geographic structure, invasive	n.r.	0.620 (mt)	0.0024	No	Chen and Hare (2011)
Acartia tonsa – lineage F	W. North Atlantic, US coast	mtDNA (COI) and nucDNA (ITS1) sequence	104	Regional	n.r.	0.974 (mt)	0.0290	No	Chen and Hare (2011)
Acartia tonsa - lineage S	W. North Atlantic, US coast	mtDNA (COI) and nucDNA (ITS1) sequence	132	Regional	n.r.	0.738 (mt)	0.0055	Yes	Chen and Hare (2011)

(*Continued*)

Table 1. Continued.

Species name	Geographic area	Marker type	Sample size	Presence and scale of structure	Pairwise F_{ST} (range)	h	pi	Dev. neutr.?	Reference
Calanus helgolandicus, C. euxinus	North Atlantic, European Seas	mtDNA sequence (16S rRNA)	316^1	Within and between basins, European Seas	0.000–0.744	0.529	0.0033	Yes	Yebra et al. (2011)
Pleuromamma xiphias	Global	mtDNA sequence (COI)	651	Within and between basins, >100s km	0.000–0.793	0.799	0.0136	Yes	Goetze (2011)
Haloptilus longicornis	Global	mtDNA sequence (COII)	1059	Within and between basins, >100s km	0–0.46	0.800	0.0200	Yes	Norton and Goetze (in press)
Other crustaceans									
Euphausia superba	Weddell Sea, Scotia Sea, Antartic Peninsula	Allozymes (7 polymorphic loci)	381	Panmixia	n.r.	N/A	N/A	N/A	Schneppenheim and Macdonald (1984)
Euphausia krohnii	W. North Atlantic, US coast, slope	Allozymes (8 polymorphic loci)	95^1	Genetic heterogeneity, but not structured	n.r.	N/A	N/A	N/A	Bucklin and Wiebe (1986)
Nematocelis megalops	W. North Atlantic, US coast, slope	Allozymes (7 polymorphic loci)	161	Genetic heterogeneity, but not structured	n.r.	N/A	N/A	N/A	Bucklin and Wiebe (1986)
Euphausia crystallorophias	Bransfield St, Elephant Is, Wedell Sea	Allozymes (6 polymorphic loci)	612	Panmixia	n.r.	N/A	N/A	N/A	Kuhl and Schneppenheim (1986)
Euphausia superba	Bransfield St, Elephant Is, Wedell Sea	Allozymes (8 polymorphic loci)	1044	Panmixia	n.r.	N/A	N/A	N/A	Kuhl and Schneppenheim (1986)
Euphausia superba	Circumpolar, Southern Ocean	Allozymes (8 polymorphic loci)	880	Panmixia	0.000–0.004	N/A	N/A	N/A	Fevolden and Scheppenheim (1989)
Meganyctiphanes norvegica	Norwegian and Greenland Seas	Allozymes (5 polymorphic loci)	1043	Panmixia	n.r.	N/A	N/A	N/A	Sundt and Fevolden (1996)
Meganyctiphanes norvegica	North Atlantic	mtDNA sequence (COI, cyt b)	101^1	Between Norwegian Sea and NW Atlantic, basin scale	n.r.	0.685 (COI), 0.908 (cyt b)	0.0038 (COI), 0.0182 (cyt b)	n.r.	Bucklin et al. (1997)
Euphausia superba	Ross Sea to Wedell Sea (4 sites)	mtDNA sequence (ND1)	249	South Georgia distinct from Wedell Sea	0.000–0.021	0.850	0.0138	Yes	Zane et al. (1998)
Meganyctiphanes norvegica	NE Alantic and Mediterranean Sea	mtDNA sequence (ND1), SSCP	1385	Between basins, European Seas	0.000–0.641	0.560	0.0038	No	Zane et al. (2000)
Euphausia crystallorophias	Davis Sea to WA Peninsula (3 regions)	mtDNA sequence (COI), SSCP	232	Genetic heterogeneity,	0.027–0.087	n.r.	n.r.	Yes	Jarman et al. (2002)

(*Continued*)

Table 1. Continued.

Species name	Geographic area	Marker type	Sample size	Presence and scale of structure	Pairwise F_{ST} (range)	h	pi	Dev. neutr.?	Reference
				but not structured					
Nematoscelis difficilis	California Current	mtDNA sequence (COI)	149	Panmixia	n.r.	0.794	n.r.	n.r.	Bucklin et al. (2002)
Meganyctiphanes norvegica	Boreal and subarctic N. Atlantic, European Seas	mtDNA sequence (ND1), SSCP	982	Primarily between basins, European Seas	0.000–0.128	0.445	0.0050	n.r.	Papetti et al. (2005)
Euphausia superba	Scotia Sea, distinct swarms	mtDNA sequence (COI)	504	Panmixia	0.000–0.022	0.999	0.0110	Yes	Goodall-Copestake et al. (2010)
Euphausia superba	Western Antarctic Peninsula	mtDNA SNPs (in cyt b, 4 sites)	585[1]	Weak or absent spatial structure, temporal differentiation	n.r.	n.r.	n.r.	n.r.	Batta-Lona et al. (2011)
Euphausia superba	Circumpolar, Southern Ocean	mtDNA sequence (ND1), Microsats	660	Panmixia	0.000–0.024	0.856	0.0139	Yes	Bortolotto et al. (2011)
Chaetognaths									
Parasagitta elegans	Japanese coastal waters	Allozymes (8 polymorphic loci)	194	Weak structure between Sea of Japan and Oyashio	n.r.	N/A	N/A	N/A	Thuesen et al. (1993)
Sagitta setosa	NE Atlantic, Mediterranean, Black Sea	mtDNA sequence (COII)	82[1]	Strong structure, between basins	n.r.	1.000	0.0221	Yes	Peijnenburg et al. (2004)
Sagitta elegans	North East Atlantic	mtDNA sequence (COII)	37[1]	Panmixia	0.000–0.177	1.000	0.0612	Yes	Peijnenburg et al. (2005)
Sagitta setosa	North East Atlantic	mtDNA sequence (COII)	32[1]	Panmixia	0.000–0.126	1.000	0.0208	Yes	Peijnenburg et al. (2005)
Sagitta setosa	NE Atlantic, Mediterranean, Black Sea	mtDNA RFLP (COII), Microsats	1739	Strong structure, between basins	0.000–0.827 (mt), 0.000–0.037 (nuc)	0.370	0.009	n.r.	Peijnenburg et al. (2006)
Cnidaria									
Pelagia noctiluca	E Atlantic, Mediterranean Sea	mtDNA (COI) and nucDNA (ITS1, ITS2) sequence	144	No structure, probable admixture between Med and Atl	0.000 - 0.095 (mt), 0.000 - 0.004 (nuc)	0.96 (mt), 0.723 (nuc)	0.0116 (mt), 0.0031 (nuc)	Yes	Stopar et al. (2010)

(*Continued*)

Table 1. Continued.

Species name	Geographic area	Marker type	Sample size	Presence and scale of structure	Pairwise F_{ST} (range)	h	pi	Dev. neutr.?	Reference
Ctenophora									
Mnemiopsis leidyi	NW Atlantic, Gulf of Mexico (non native areas: Eurasia)	Microsatellites (6 loci used)	467	Between two source populations (New England, Gulf of Mexico)	0.000–0.268	N/A	N/A	n.r.	Reusch et al. (2010)

Only studies that address population subdivision and genetic structure are included. Columns are: Species name, including specific genetic lineages if relevant; Geographic area, the geographic coverage of sampling; Marker type, the genetic marker(s) used to infer population structure; Sample size, for the species listed only, in allozyme studies this is the maximum number of alleles for any locus/2 (typically reported as No. alleles surveyed, not individuals); Presence and Scale of Structure, the geographic scale over which population structure was inferred to occur; Pairwise F_{ST}, range of F_{ST} values among individual population samples; h, haplotype diversity; pi, nucleotide diversity; Neutr?, if significant deviations from neutrality were observed in Tajima's *D*, Fu and Li's, or Rozas's R^2 tests. Note that calculations of h, pi, and neutrality tests are only applicable to mtDNA markers because these are haploid and hence gametic phase is known. N/A, not applicable; n.r., not reported; NS, nonsignificant.

In the sample size column indicates studies in which over 1/4 of the population samples had $N < 15$ individuals sampled. Inferences of population structure may be influenced by low sample size in these studies.

genetic isolation often is observed across distinct pelagic biomes even in these entirely planktonic taxa.

Selection as a Dominant Evolutionary Force

One important misinterpretation that has supported the view of low evolutionary potential in marine zooplankton is the relative unimportance of genetic drift in influencing allele frequencies in large populations, according to standard population genetic models (Crow and Kimura 1970). However, relatively little attention has been paid to the reverse side of this coin, namely that selection is highly effective in large populations. The reasons for the higher efficacy of selection are twofold. First, more adaptive mutations occur in large populations, simply because there are more individuals to undergo mutation (e.g., Lynch et al. 1991; Barton 2010). Furthermore, beneficial mutations are common enough in large populations to arise both recurrently and on independent genetic backgrounds, increasing the chance that they arrive at the right time, place, and on the appropriate genetic background (Pennings and Hermisson 2006a,b; Ralph and Coop 2010). Second, selection is more effective because the stochastic effect of drift is smaller in large populations (e.g., Gillespie 1999, 2000, 2001; Charlesworth 2009). A simple theoretical model (Fig. 2) demonstrates how even very mild, immeasurably small, selection pressures ($s = 10^{-9}$ to 10^{-15}) can quickly drive beneficial mutations to fixation at population sizes typical of marine zooplankton ($N_e = 10^7$ to 10^{15}; Fig. 2). Figure 2 also shows that with increasingly large populations, the selection coefficients that have a substantial effect with respect to substitution rate become progressively smaller. Therefore, the assumption of neutrality will be more likely violated in species with large populations. Even though there is still active debate as to whether most of the genetic variation within and between species is selectively neutral (Kimura 1968, 1983), or whether a large proportion of the variation is subject to selection (Gillespie 1991; Hahn 2008; Wares 2010), we argue here that selection may be a dominant force in the evolution of open ocean plankton, because they are at the extreme end of the scale in terms of population size of marine organisms. The effect of population size is illustrated by genome-wide studies in terrestrial model organisms that reported substantial evidence of adaptive evolution in *Drosophila* and *Escherichia coli* (large populations), whereas genetic variation in *Homo sapiens* and *Arabidopsis* (small populations) conformed to a background selection model, with a large number of segregating deleterious polymorphisms (reviewed in Hahn 2008). Barton (2010) and Karasov et al. (2010) have also argued that adaptation is not mutation limited in very large pop-

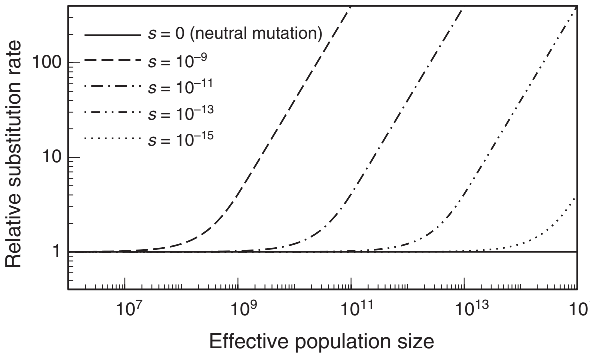

Figure 2. Selection in large plankton populations. Results from a model derived from standard population genetics theory (Crow and Kimura 1970) showing that substitution rate is sensitive to small selection coefficients in large populations. For slightly beneficial mutations with selection coefficient (*s*), the fixation probability (*P*) can be approximated by:

$$P(s,N) = \frac{1 - e^{-2s}}{1 - e^{-4Ns}}$$

where *N* is diploid effective population size. When *s* converges to 0 (i.e., mutations are neutral) *P* is 1/2*N* and as *s* grows larger *P* becomes approximately 2*s*. For simplicity we assume that the substitution rate can be described as the number of mutations arising times the fixation probability. The substitution rate, relative to the neutral substitution rate, is plotted as a function of effective population size for various immeasurably small selection coefficients (ranging from 10^{-9} to 10^{-15}). This model ignores clonal interference, that is, competition between beneficial mutations, which is expected to slow down the response to selection in asexual species (e.g., Gerrish and Lenski 1998).

ulations, and that rapid appearance of adaptive alleles can enable fast evolution, for example, adaptation to insecticide in *Drosophila* within 50 years, or ~1000 generations.

Thus far, no studies of open ocean zooplankton have directly addressed the question as to how pervasive selection is in driving evolutionary change in natural populations (but see Dam 2013 and Sanford and Kelly 2011 for selected examples from coastal zooplankton and benthic invertebrates with meroplanktonic larvae). One interesting conclusion from Sanford and Kelly (2011) was that species with planktonic dispersal comprise a surprisingly high percentage (66%) of the marine invertebrates known or suspected of exhibiting local adaptation. Several studies of pelagic marine fish have indicated a much more important role for selection than was previously thought (e.g., Hauser and Carvalho 2008; Gaggiotti et al. 2009; Bradbury et al. 2010; but see McCusker and Bentzen 2010), and selection experiments with the coccolithophore *Emiliania huxleyi* have shown that adaptive evolution to ocean acidification can occur within ~500 generations (Lohbeck et al. 2012).

Three lines of evidence suggest that selection may be a particularly important driver of evolution in open ocean zooplankton. First, if selection works efficiently in large populations, we would expect the assumption of neutrality to be violated often in studies of marine zooplankton. Indeed, we do commonly see significant deviations from neutrality across a broad array of planktonic taxa, with 16 of 21 studies reporting nonneutral evolution based on Tajima's *D*, Fu and Li's, or Rozas's R^2 tests (Table 1). However, it is well known that these commonly applied neutrality tests (e.g., Tajima's *D* test, Tajima 1989) are sensitive to fluctuations in population size (e.g., Simonsen et al. 1995; Nielsen 2005), and significant results have often been interpreted in this context. The causative factors that underlie departures from neutrality therefore remain largely unknown, but could indicate that selection commonly influences the extent and distribution of genetic variation in marine zooplankton populations (see also Wares 2010). Broader investigation of these patterns is warranted, and we call for consistent inclusion of rigorous tests of neutrality (see e.g., Nielsen [2005] for a review) as a standard component of data analyses, such that it will be possible to assess how commonly the neutrality assumption is violated across taxa and loci. The McDonald–Kreitman (MK) test (Mcdonald and Kreitman 1991) is particularly informative in cases where multiple protein-coding sequences of related species are available, because this test is robust to demographic assumptions (Nielsen 2001). The MK test is based on the prediction of neutral theory that the ratio of replacement (nonsynonymous) to silent (synonymous) *fixed differences* observed between species should equal the ratio of replacement to silent *polymorphisms* within species. A significant excess of replacement fixed differences relative to silent changes is interpreted as evidence for adaptive evolution. To our knowledge, only one study of open ocean zooplankton has applied this test (Peijnenburg et al. 2005), and it reported significant evidence for selection acting on the mitochondrial cytochrome oxidase II gene in two chaetognath species.

A second line of evidence suggesting that selection may be an important driver of evolution in species with large populations is the finding of large discrepancies between census and effective population sizes, which are commonplace for marine species (Grant and Bowen 1998; Avise 2000; Hauser and Carvalho 2008; Portnoy et al. 2009). Such discrepancies would be expected under widespread deviations from the neutral model. Studies of marine zooplankton that have contrasted census and effective population sizes, as estimated from abundance and genetic data, respectively, have reported dramatic differences ranging from 10^{8} to 10^{10} fold in chaetognaths (Peijnenburg et al. 2005), copepods (Bucklin and Wiebe 1998), and krill (Zane et al. 1998; but see Zane et al. 2000, reported a threefold difference). All of these studies used mitochondrial DNA to estimate effective population sizes, which, if under selection, would be expected to result in lower estimates of N_e relative to 'true' N_e, as estimated from neutral markers. Recent work has also shown that a key prediction of the neutral theory, namely that species with large populations should have more genetic diversity than species with small populations, does not hold for mitochondrial DNA (Bazin et al. 2006), and this observation was explained by the influence of pervasive selection on the mitochondrial genome (see also Meiklejohn et al. 2007; Galtier et al. 2009; Wares 2010). Similarly for the nuclear genome, levels of genetic diversity across the tree of life do not scale with species abundances, which is inconsistent with a neutral model of evolution (Lynch 2006; Hahn 2008).

Third, and finally, as the strength and type of selection will differ between unlinked genetic markers, we would expect to see large differences in the degree of population structure detected by different loci if selection is an important driver of genetic differentiation (see also Fig. 2 and Piganeau et al. 2011). Very few studies of zooplankton population structure have incorporated multiple unlinked genetic markers (Table 1), making it difficult to evaluate how common such discrepancies are. One study that contrasted mitochondrial and nuclear variation in a planktonic chaetognath reported large differences in the degree of structure detected by the two marker types (Peijnenburg et al. 2006). The historical heavy reliance on mtDNA markers in plankton population genetic studies has limited our ability to detect selection, and further tests of the ideas outlined above will become possible as the field moves toward genome-wide data and direct comparisons across loci and taxa. We do not yet have a representative view of the amounts of genomic diversity present in plankton populations and it remains to be tested whether selection models (and what types of model) or classical models of genetic drift are most appropriate to describe molecular evolution in zooplankton.

Genetic Isolation in Open Ocean Habitats

One important supporting argument for the idea that zooplankton are slowly evolving is that high dispersal rates limit their capacity to evolve adaptively in response to spatially varying selection (e.g., Grosberg and Cunningham 2001). But what is known regarding dispersal and connectivity among populations of open ocean zooplankton?

Early genetic research on the population structures of planktonic species often did support the view of nearly unlimited dispersal. Initially, workers focused on ecologically important, keystone species, and usually found genetic homogeneity among samples from distant areas of the distributional range. For example, *Euphausia superba*, the keystone euphausiid of the Antarctic pelagic ecosystem, has been a target species for population genetic studies dating back to the mid 1980s (e.g., Table 1; MacDonald et al. 1986; Fevolden and Scheppenheim 1989; Bortolotto et al. 2011). Although a number of studies reported weak but significant population structure (Fevolden and Ayala 1981; Zane et al. 1998; Batta-Lona et al. 2011), these patterns disappeared in more rigorous work with higher sample size and higher resolution genetic markers (Fevolden and Scheppenheim 1989; Bortolotto et al. 2011). Based on current evidence, it appears that this species is panmictic throughout its range. Note, however, that with even more powerful data (e.g., thousands of Single Nucleotide Polymorphism (SNP) loci accessed using Next Generation Sequencing technologies) it may well be that the null hypothesis of genetic homogeneity is ultimately rejected. Studies on *Calanus finmarchicus*, the dominant planktonic copepod in the boreal North Atlantic, followed a similar trajectory, with a number of reports of weak but significant differentiation between gyre systems and at basin spatial scales (Table 1; Bucklin and Kocher 1996; Bucklin et al. 2000a; Unal and Bucklin 2010). However, using a powerful combination of mitochondrial and nuclear microsatellite loci, Provan et al. (2009) demonstrated that the species lacks population genetic structure across the North Atlantic (Provan et al. 2009). A number of studies on other holoplanktonic organisms also have hinted at high dispersal rates, including a notable series of studies on planktonic foraminifers that found identical genotypes across different ocean basins worldwide (de Vargas et al. 1999, 2001, 2002, 2004; note that isolation is also seen in this group, e.g., Aurahs et al. 2009; Ujiie et al. 2012; Seears et al. 2012). In combination, this body of work has demonstrated that there probably *are* some holoplanktonic species that are panmictic throughout their distributional range. However, we argue here that the population structure of these hyper-abundant species may not be typical of the broader planktonic fauna, and an early focus on these species has inappropriately instilled the sense that holoplankton have universally high dispersal capacity.

The emerging patterns from genetic results on a broader array of species suggest a more complex and nuanced picture of dispersal and connectivity among populations of open ocean zooplankton. First, there is strong evidence for spatial genetic structure and limited gene flow among populations in a number of plankton species, with distributions ranging from coastal seas to open ocean habitats. For example, planktonic chaetognaths and copepods have been shown to have restricted dispersal in the coastal ocean (Peijnenburg et al. 2004, 2006; Papadopoulos et al. 2005; Unal et al. 2006;

Chen and Hare 2011; Yebra et al. 2011), with rare multilocus studies providing the most compelling evidence for limited gene flow among European basins (Peijnenburg et al. 2006; Reusch et al. 2010). Truly oceanic species also have been found to harbor a number of genetically very distinct populations (Goetze 2005, 2011; Papetti et al. 2005; Nelson et al. 2009), with sample sizes sufficiently high to characterize the distribution of genetic variation at mesoscale (10s to 100s of km) to ocean basin spatial scales (>1000 km). If spatial genetic structure is interpreted in light of gene flow, these studies imply a much more limited dispersal range than expected for holoplanktonic organisms in open ocean habitats (e.g., Goetze 2011). Nonmetazoan holoplankton also exhibit strong spatial genetic structure in a number of cases, implying that dispersal may be more limited than initially expected across a broad diversity of planktonic life (e.g., Darling et al. 2007; McCauley et al. 2009; Rynearson et al. 2009; Casteleyn et al. 2010; Ujiie et al. 2012; Whittaker et al. 2012).

A second emerging insight is that among zooplankton species with circumglobal or cosmopolitan biogeographic ranges, spatial genetic structure often occurs at the scale of pelagic biomes. For example, studies on the copepods *Eucalanus hyalinus*, *E. spinifer*, *Pleuromamma xiphias*, and *Haloptilus longicornis* all report genetic homogeneity among sample sites within subtropical gyres, with strong and significant population genetic breaks occurring between subtropical gyres and ocean basins (Goetze 2005, 2011; Norton and Goetze in press). These results imply limited dispersal across equatorial waters in all of these species, irrespective of whether or not the species is antitropical in distribution (*Eucalanus* species are antitropical, *Pleuromamma* and *Haloptilus* spp. are not). In these cases (and others), barriers to dispersal in the open sea occur at oceanographic regions with sharp transitions in both biotic and abiotic properties (Thornhill et al. 2008; Goetze 2011; Norton and Goetze in press), and are likely bio-physical in nature.

Third and finally, increasingly it appears that population genetic structure is species-specific in marine zooplankton, with closely related species often showing very different patterns of differentiation across the same pelagic habitats (Goetze 2005; Blanco-Bercial et al. 2011; Chen and Hare 2011). These results suggest that there are differences between species in realized dispersal, which may be linked to species-specific ecological or habitat requirements. For example, Chen and Hare (2011) documented salinity differences in the preferred habitat of three highly divergent lineages within *Acartia tonsa* that likely played a role in the development of phylogeographic structure within each of these cryptic species. The genetic lineage found in estuarine habitats showed high phylogeographic divergence among coastal embayments (US Atlantic coast), while the most oceanic lineage entirely lacked population genetic structure across the same sampling sites. Similar ecophysiological mechanisms likely control dispersal among populations of open ocean zooplankton, though there are no studies that have examined this for truly oceanic taxa. What constitutes optimal habitat will vary across species, with the nature of dispersal barriers highly dependent on the ecological niche of the organism. Therefore, it is more appropriate to consider population genetic structure a species-specific trait that varies across holoplanktonic taxa, as does any other ecological or life history trait, than to view the zooplankton as monotypically 'high dispersal' species.

This emerging view of the complexity of dispersal in marine zooplankton extends a number of observations that have been made in other marine species to the pelagic habitat. Panmixia was once expected for all marine species with large population size and a planktonic phase of the life history (e.g., Palumbi 1992, 1994). This idea now has been discarded as overly simplistic for both marine fish and benthic invertebrates (with meroplanktonic larvae), with extensive empirical studies having shown 'closed' marine populations and adaptive responses to human-induced and natural environmental change (e.g., Conover et al. 2006; Hauser and Carvalho 2008; Cowen and Sponaugle 2009; Hellberg 2009; Marshall et al. 2010; Sanford and Kelly 2011). There is now considerable evidence that many open ocean zooplankton species also demonstrate population genetic differentiation across distinct pelagic habitats, an observation that has important implications regarding their capacity to respond to local selective forces.

New Views on Marine Zooplankton Evolution

Given the findings and arguments outlined above (on selection and genetic isolation), we hypothesize that open ocean zooplankton have large adaptive potential and may be capable of strong evolutionary responses (genetic adaptation) to changing ocean conditions. These responses could be rapid, occurring on ecological time scales (Hairston et al. 2005; Schoener 2011), and are thus important to consider in discussions about responses of the ocean's biota to contemporary climate change (Davis et al. 2005; Parmesan 2006). Significant findings of spatial population structuring in zooplankton (Table 1) imply that selection could drive fitness toward a phenotypic optimum for ocean conditions experienced within a particular oceanographic habitat (e.g., a subtropical gyre), rather than across the range of environmental conditions that occur throughout the distribution of any particular species (often circumglobal in subtropical and tropical waters). This is important, as evolution can then trend toward specialization on specific ocean habitats rather than toward phenotypic plasticity or ecological generalism. In addition, marine zooplankton have short generation times, which can play a critical role in the rate of evolutionary change (e.g., Thomas et al. 2010), and have been shown capable of very rapid evolution in peripheral marine environments (Dawson and Hamner 2005) and during habitat invasions (Lee et al. 2011, and references therein). These observations suggest that zooplankton can show rapid responses to selection under appropriate conditions.

One implication of our hypothesis is that marine zooplankton may have a more limited capacity to track suitable habitat under changing ocean conditions than is currently assumed (e.g., Provan et al. 2009; Ji et al. 2010; Reygondeau and Beaugrand 2010). Results from the continuous plankton recorder (CPR) survey have convincingly demonstrated that range shifts are occurring at the northern boundary of the distribution of many temperate and boreal North Atlantic species in response to warming ocean conditions (Beaugrand et al. 2002, 2009; Beaugrand 2003; Beaugrand and Reid 2003). However, many of the species within the CPR record have distributions that extend across a range of pelagic biomes (e.g., subtropical gyres, boundary current, and equatorial upwelling ecosystems), and nothing is currently known regarding dispersal within and among different areas of their distribution. These species may in fact consist of a global collection of semi-isolated populations that respond individually to the changing distribution of their preferred habitat. Also, because the presence and strength of barriers to dispersal are expected to be species-specific for marine zooplankton (see above), the capacity of a species to track suitable habitat may vary across taxa and may lead to shifting community structure and trophic mismatches in pelagic foodwebs (e.g., as observed in the North Sea, Beaugrand et al. 2003; Reygondeau and Beaugrand 2010).

Priorities for Future Research

Currently, very little is known about adaptation of zooplankton to local oceanographic conditions. Testing our hypothesis of high evolutionary potential in open ocean zooplankton will require research in at least two primary areas. First, the question of how pervasive natural selection is in driving population divergence in zooplankton needs to be addressed. Second, the spatial and temporal scales over which differentiation occurs in the open ocean need to be rigorously quantified. Next Generation sequencing (NGS) technologies have made possible the rapid generation of large-scale sequence data from non-model organisms at reasonable cost. We expect that these technologies (reviewed elsewhere in e.g., Davey et al. 2011) and in particular Restriction-site associated DNA sequencing (RADSeq, Davey and Blaxter 2011) will enable the field to move away from single marker studies (some fine examples of this approach include Emerson et al. 2010; Hohenlohe et al. 2010; Wagner et al. 2013).

Indirect approaches can be used to address the question as to how pervasive selection is in driving the evolution of open ocean zooplankton (taxa that typically cannot be cultured in the lab). One cost-effective approach to examining adaptive variation in natural populations is to study functionally important traits related to, for instance, morphology or life history. Differentiation at these quantitative traits is typically expressed as Q_{ST} or P_{ST} (e.g., Merilä and Crnokrak 2001; McKay and Latta 2002; Leinonen et al. 2008) and can be compared to patterns of differentiation at neutral genetic markers, which are typically expressed as F_{ST}. If $Q_{ST} > F_{ST}$, diversifying selection is invoked, in which different phenotypes are favored in different populations. Whereas if $Q_{ST} < F_{ST}$, this suggests stabilizing selection, and the same phenotype is favored across populations. Another indirect approach would be to use genome scans to contrast adaptive and neutral variation across the genome (e.g., reviewed in Davey et al. 2011). By comparing divergent populations, it is possible to identify loci showing signatures of selection using, for instance, outlier analyses, cline analyses, or tests of selection based on ratios of neutral and adaptive changes (reviewed in e.g., Nielsen 2005; Nielsen et al. 2009; Rice et al. 2011). A third indirect approach is the candidate gene approach, in which specific loci (genes) of known functional significance are sequenced. A nice example is provided by Larmuseau et al. (2009) in which a sensory gene, rhodopsin, was sequenced for sand goby individuals from different populations in Europe. They found that sequences of this gene did not cluster according to geographical or historical proximity, but according to the general photic conditions of the habitat of the fish. Zooplankton populations sampled along naturally occurring gradients of temperature, salinity, or acidification, which change with latitude and/or depth, could be examined for sequence variation at neutral as well as targeted genetic loci. An example of a genome-wide approach can be found in Bradbury et al. (2010), in which a survey of single nucleotide polymorphisms in Atlantic cod was used to pinpoint 40 loci for which allele frequencies showed parallel temperature-associated clines in the eastern and western north Atlantic. Note that the effect of selection is inferred indirectly using these methods and additional experiments (e.g., laboratory, mapping, and/or gene expression studies) would be necessary to link genetic loci with specific targets of selection (see Feder and Mitchell-Olds' [2003] perspective on the emerging field of evolutionary and ecological functional genomics [EEFG] which seeks to understand the functional basis of evolutionary forces shaping ecologically important traits in natural biological communities). Once several comparative genome-wide datasets become available from natural populations of planktonic taxa, we can begin to draw more general conclusions about the levels of intraspecific and intragenomic genetic variability and the relative importance of selection.

In order to rigorously quantify the spatial and temporal scales over which differentiation occurs in the open ocean, we need to substantially increase the types and amounts of data that are collected. First, it is critically important to be able to compare genetic results across marker types in order to obtain rigorous estimates of dispersal through Bayesian, Maximum Likelihood, or coalescent analytical techniques (e.g., Pritchard et al. 2000; Hey and Nielsen 2004; Zhang 2008; Beerli and Palczewski 2010; Hey 2010; Nielsen et al. 2012). The historical dominance of single marker studies has limited our capacity to distinguish demographic forces (migration, changing population size) from selection. Second, limited sampling in terms of the number of individuals sampled per population (Table 1), but also across space and time, has resulted in low scientific rigor in some studies. Revealing the amounts of genetic variation present within populations is particularly important, because this is a critical component to assessing evolutionary potential (e.g., Chevin et al. 2010). In addition, temporal variability needs to be more comprehensively addressed in future work, as nearly nothing is known regarding the stability of zooplankton population structure through time (but see Peijnenburg et al. 2006 and Bortolotto et al. 2011 as rare examples of studies with time-stratified sampling). Third, and finally, resolving spatial patterns of gene flow for a greater diversity of species is also paramount to understanding the nature of dispersal barriers for marine zooplankton. Current evidence suggests that realized dispersal for holoplanktonic species may be linked to the ecological niche of the organism, and this idea needs to be tested with community-wide data on population genetic structures of a diverse panel of species with distinct pelagic niches. Ideally, such species should be collected on the same research cruises so that comparable spatial and temporal scales are sampled. Another approach would be to compare population genetic structures of related species with different life history or ecological characteristics as is common in the benthic invertebrates research community.

Finally, a wide range of questions on the fundamental basis of evolutionary change in marine zooplankton remain to be addressed. We hope that the ideas outlined here, in combination with the suite of high-throughput genomics techniques now available for development of genome-wide markers in nonmodel species will catalyze research in this field.

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Conflict of Interest

None declared.

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