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The geographic problem in cephalopod genomics

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Publications describing genomes of various cephalopod species have recently proliferated. Some papers have involved large geographic distances between the collection locality of sequenced specimens and the type locality of the presumed species. However, cryptic species have been demonstrated in many cephalopods. Therefore, even if the sequenced specimen is very similar morphologically to the species in question, the likelihood that it is a member of the species in question decreases with increasing distance from the type locality. An associated problem is that many publications do not provide information adequate to determine the source locality for the genomic sequence. We reviewed a decade of literature on mitochondrial genomes of cephalopods and found a total of 43 publications containing 48 species within 23 genera. Of the 48 species, only 17 could be evaluated for our geographic question. Distances between sampling locality and type locality of the named species ranged from 0 nautical miles (sampled at type locality) to half-way around the world. Where data were present for distance calculation, the average for the 17 species was 3785 km (2044 nmi).

KEYWORDS

biogeography, genomics, species complex, type locality, sampling

Introduction

Determination of genetic sequences has revolutionized understanding of evolutionary relationships. Increasingly sophisticated methods have allowed this revolution to progress greatly throughout the last few decades to include inferences about entire genomes. Accordingly, the literature describing cephalopod genomes, especially those of the mitochondria, has increased greatly over the past 10 years (O'Brien, 2018). The primary goal of most of these publications has been to resolve phylogenetic relationships within extant Cephalopoda.

Another result of widespread use of genetic sequencing, including “barcodes” and other sequences shorter than entire genomes, has been an increasing recognition that

species with distributions once considered to be very broad or even global were actually complexes of morphologically similar species with geographic ranges resembling a patchwork within the broad range of the species complex. Some examples include taxa within the families Sepiolidae (Fernandez-Alvarez et al., 2021), Loliginidae (Sales et al., 2017), Ctenopterygidae (Escanez et al. (2018), Ommastrephidae (Fernandez-Alvarez et al., 2020; Xu et al., 2020a), Spirulidae (Hoffmann et al., 2021), and Octopodidae (Avendano et al., 2020; Amor and Hart, 2021). Because of these species complexes, both currently recognized and possibly to be discovered in the future, a substantial potential exists for misidentification of specimens collected for genomic sequencing (e.g., Lima et al., 2017; Salvi et al., 2021). This misidentification potential is especially true if the genomic specimen is not collected within the normal range of nominal sequenced species (i.e., named based on morphological identification). We are concerned that authors, using specimens from the nearest convenient area to sample a presumed species or from sources where the actual collection locality cannot be verified (e.g., fish markets,

aquarium dealers), could be using a different species than what they report and, as a result, sequences in genomic databases may be misidentified.

Materials and methods

We surveyed the past decade of genomic literature on Cephalopoda for comparison of collection locality with designated type localities of the nominal species to determine the extent of this potential problem. Only publications describing complete mitochondrial genomes were analyzed. Each publication was examined to determine the collection locality of the specimen used for genomic analysis. Type localities for the nominal species are available online. We converted both sample locality and type locality to latitude/longitude and then calculated distance between them using NOAA Latitude/Longitude Distance Calculator (<https://www.nhc.noaa.gov/gccalc.shtml>). The repository and accession numbers for published genome sequences were also recorded (Table 1).

TABLE 1 Mitochondrial genome sequences for cephalopods in recent literature.

| Species | Reference | Genome repository | Locality of specimen | Type locality of species | Separation* |
|---------------------------------|----------------------------|-----------------------|-------------------------------------|--------------------------------|-------------|
| <i>Nautilus pompilius</i> | Wang et al., 2018 | GenBank KY794928 | Not given | Ambon Island, Indonesia | n/a |
| <i>Sepia officinalis</i> | Akasaki et al., 2006 | GenBank AB240155 | Tsukiji Fishery Market, Japan | "Oceano" [NE Atl. O.] | n/a |
| <i>Sepia aculeata</i> | Guo et al., 2016 | GenBank KF690633 | Not given | Java, Indonesia | n/a |
| <i>Sepia apama</i> | Kawashima et al., 2013 | GenBank AP013073 | Not given | Port Adelaide, Australia | n/a |
| <i>Sepia esculenta</i> | Yokobori et al., 2007 | DDBJ genbank AB266516 | Tsukiji Fishery Market, Japan | Yokohama Fishery Market, Japan | n/a |
| <i>Sepia latimanus</i> | Kawashima et al., 2013 | GenBank AP013074 | Not given | Port Dorey, New Guinea | n/a |
| <i>Sepia latimanus</i> | Lu et al., 2019 | GenBank MK347498 | Naozhou, China | Port Dorey, New Guinea | 1890 |
| <i>Sepia lycidas</i> | Kawashima et al., 2013 | GenBank AP013075 | Not given | Canton Fishery Market, China | n/a |
| <i>Sepia lycidas</i> | Guo et al., 2018 | GenBank KJ162574 | Zhanjiang fishing grounds, SE China | Canton Fishery Market, China | n/a |
| <i>Sepia pharaonis</i> | Kawashima et al., 2013 | GenBank AP013076 | Not given | Gulf of Suez, Red Sea | n/a |
| <i>Sepia pharaonis</i> | Song et al., 2021 | ERZ1300763 | Ningbo City fishfarm, China | Gulf of Suez, Red Sea | n/a |
| <i>Sepia pharaonis</i> | Wang et al., 2014 | GenBank KC632521 | Not given | Gulf of Suez, Red Sea | n/a |
| <i>Metasepia tullbergi</i> | Lee et al., 2021 | GenBank MT974497 | NE Taiwan | Nagasaki, Japan | 632 |
| <i>Sepiella inermis</i> | Wang et al., 2015 | GenBank KF040369 | Not given | Bombay [Mumbai], India | n/a |
| <i>Sepiella maindroni</i> | Zheng et al., 2016 | GenBank KR912215.1 | Not given | Pondichery, India | n/a |
| <i>Semirossia patagonica</i> | Kawashima et al., 2013 | GenBank AP012226 | Not given | Portland Bay, Patagonia | n/a |
| <i>Spirula spirula</i> | Strugnell et al., 2017 | GenBank KU893141 | Queensland, Australia | America | n/a |
| <i>Loligo beka</i> | Jiang et al., 2016e & 2018 | GenBank KT254309 | 30.1°N 122.4°E, E. China Sea | Kojima Bay, Japan | 585 |
| <i>Loligo chinensis</i> | Jiang et al., 2017b & 2018 | GenBank KT362380 | 30.1°N 122.4°E, E. China Sea | Canton Fishery Market, China | n/a |
| <i>Loligo duvauceli</i> | Jiang et al., 2016a & 2018 | GenBank KR051264 | 30.1°N 122.4°E, E. China Sea | Syntypes India & Sumatra | n/a |
| <i>Loligo edulis f. budo</i> | Takemoto & Yamashita, 2012 | GenBank AB675081 | Multiple locations | Multiple locations, Japan | n/a |
| <i>Loligo edulis f. kensaki</i> | Takemoto & Yamashita, 2012 | GenBank AB675080 | Multiple locations | Multiple locations, Japan | n/a |
| <i>Loligo japonica</i> | Jiang et al., 2017b & 2018 | GenBank KU568467 | Hakodate, Japan | Yokohama Fishery Market, Japan | n/a |

(Continued)

TABLE 1 Continued

| Species | Reference | Genome repository | Locality of specimen | Type locality of species | Separation* |
|-----------------------------------|-----------------------------|-------------------------|----------------------------------|-----------------------------------|-----------------|
| <i>Loligo opalescens</i> | Jiang et al., 2016d & 2018 | GenBank KP336703 | 30.1°N 122.4°E, E. China Sea | Puget Sound, Washington, USA | 4975 |
| <i>Uroteuthis chinensis</i> | Xu et al., 2020b | GenBank MN687903 | Minnan–Taiwan Bank | Canton Fishery Market, China | n/a |
| <i>Loliolus (N.) uyii</i> | Jiang et al., 2016b & 2018 | GenBank KP265013 | 30.1°N 122.4°E, E. China Sea | Kagoshima Bay, Japan | 432 |
| <i>Sepioteuthis lessoniana</i> | Akasaki et al., 2006 | GenBank AB240154 | Tsukiji Fishery Market, Japan | Not designated | n/a |
| <i>Watasenia scintillans</i> | Akasaki et al., 2006 | GenBank AB240152 | Tsukiji Fishery Market, Japan | Misaki[?], Japan | n/a |
| <i>Watasenia scintillans</i> | Hayashi et al., 2016 | GenBank KJ845633 | Toyama Bay, Japan | Misaki[?], Japan | n/a |
| <i>Chiroteuthis picteti</i> | H. Kim et al., 2018 | GenBank MG833837 | east sea of Korea | Ambon Island, Indonesia | 2450 |
| <i>Bathyteuthis abyssicola</i> | Kawashima et al., 2013 | GenBank AP012225 | Not given | 46°16'S 48°27'E, Southern Ocean | n/a |
| <i>Thysanoteuthis rhombus</i> | Tang et al., 2021 | GenBank MT733875 | South China Sea | Strait of Messina, Sicily | 5070 |
| <i>Illex argentinus</i> | Jiang et al., 2016c | GenBank KP336702 | Not given | Patagonia, 39°S 55°W | n/a |
| <i>Todarodes pacificus</i> | Akasaki et al., 2006 | GenBank AB240153 | Tsukiji Fishery Market, Japan | Hokodate, Japan | n/a |
| <i>Sthenoteuthis oualaniensis</i> | Xu et al., 2020c | GenBank MT661575 | 17°59'N 111°59'E, China Sea | Oualan Island, Caroline Islands | 3080 |
| <i>Vampyroteuthis infernalis</i> | Yokobori et al., 2007 | DDBJ genbank AB266515 | Ogasawara Island Chain, Japan | 1°56.7'S 7°40.6'E, Atlantic Ocean | 7715 |
| <i>Amphioctopus aegina</i> | Zhang et al., 2017 | GenBank KT428877 | Haikou Fishery Market, China | Not designated | n/a |
| <i>Amphioctopus fangsiao</i> | Lashari et al., 2020 | GenBank MF029678-029691 | 9 separate localities in China | Japan | n/a |
| <i>Amphioctopus marginatus</i> | Tang et al., 2018 | GenBank KY646153 | Haikou Fishery Market, China | Kamae, Oita Prefecture, Japan | n/a |
| <i>Amphioctopus neglectus</i> | Tang et al., 2019 | GenBank MF447873 | Nanning Fishery Market, China | Ko Phuket, Thailand | n/a |
| <i>Amphioctopus rex</i> | Tang et al., 2019 | GenBank MF447874 | Wenzhon Fishery Market, China | Ko Food, Trat Province, Thailand | n/a |
| <i>Octopus bimaculatus</i> | Dominguez et al., 2016 | GenBank KT581981 | N. Gulf of California, Mexico | Syntypes; 3 localities | n/a |
| <i>Octopus conispadiceus</i> | Ma et al., 2016 | GenBank KJ789854 | Haishenwai, Amur Bay, Russia | Sapparo Fishery Market, Japan | n/a |
| <i>Octopus dollfusi</i> | Yan et al., 2018 | GenBank KX108697 | Zhanjiang, Guangdong, China | "Indochina" | n/a |
| <i>Octopus fitchi</i> | Magallon-Gayon et al., 2020 | GenBank MK450541 | Bahia Magdalena, Mexico | N. Gulf of California, Mexico | 990 |
| <i>Octopus minor</i> | B. Kim et al., 2018 | SRA database SRX3462978 | Not given | Suruga Bay, Japan | n/a |
| <i>Octopus minor</i> | Cheng et al., 2012 | GenBank HQ638215 | Weihai, Shandong Province, China | Suruga Bay, Japan | 785 |
| <i>Octopus mimus</i> | Magallon-Gayon et al., 2020 | GenBank MN078094 | Zihuatanejo, Guerrero, Mexico | Iquique, Chile | 2925 |
| <i>Octopus ocellatus</i> | Akasaki et al., 2006 | GenBank AB240156 | Tsukiji Fishery Market, Japan | "China Sea" | n/a |
| <i>Octopus sinensis</i> | Li et al., 2021 | GenBank MT712046 | Zhoushan, China | Oyano Island, Ariake Sea, Japan | 446 |
| <i>Octopus vulgaris</i> | Zarrella et al., 2019 | Not listed | Bay of Naples, Italy | "Mediterranean Sea" | n/a |
| <i>Cistopus chinensis</i> | Cheng et al., 2013 | GenBank KF017606 | coastal Xiamen, China | Xiamen, China | 0! |
| <i>Cistopus taiwanicus</i> | Cheng et al., 2013 | GenBank KF017605 | "coastal Taiwan" | Miaoli, Taiwan | close+/- |
| <i>Hapalochlaena fasciata</i> | Kim et al., 2020 | GenBank MT497543 | Southern coastal Korea | Port Jackson, Australia | 1165 |
| <i>Hapalochlaena maculosa</i> | Morse et al., 2018 | Not listed | 8 South Australia localities | "Australia" | n/a |
| <i>Argonauta argo</i> | Hirota et al., 2021 | DDBJ genbank LC596061 | Oki Island, Sea of Japan | Syntypes; Red Sea + Mediterranean | n/a |
| <i>Argonauta hians</i> | Chiu et al., 2018a | GenBank KY649285 | Kenting, Taiwan | Ambon Island, Indonesia | 1600 |
| <i>Tremoctopus violaceus</i> | Chiu et al., 2018b | GenBank KY649286 | Taiwan | Not designated | n/a |

Approx. distance between specimen location and type locality calculated using <https://www.nhc.noaa.gov/gccalc.shtml> Separation* is calculated as nmi. (1nmi = 1.852 km). Shaded boxes: data absent or too general to be analyzed.

Bold numbers in the last column highlight the publications for which included information was adequate for distance calculation.

Results

An online search of the previous ten years of Cephalopoda genomic literature found a total of 58 genomic descriptions within 43 publications containing 48 different species in 23 genera (Table 1). For many species sequenced (70%), either collection locality or type locality (from the original description) was missing or was too general (e.g., Australia). In addition, if either locality was indeterminate (e.g., Tsukiji fishery market); or there were multiple type localities (ex. syntypes); or the genome was derived from combined specimens from multiple localities, the sequence was not included in our distance analysis.

Of the 48 species sequenced, only 17 could be evaluated for our geographic question (Table 1). Distances calculated ranged from 0 km (sampled at type locality) to half-way around the world in a different ocean basin. The average distance between sampling locality and type locality for the 17 species for which data were adequate for distance calculation, was 3785 km (2044 nm).

Incidentally, as we reviewed this literature for geographic information, we also noticed that very few of the publications included any indication that voucher specimens or unprocessed tissue were preserved in established archival collections for future research. For example, of the 17 species mentioned above, only 5 (29.4%) had vouchered specimens. Thus, 10.4% of species accounts included both adequate geographic information and archived specimens.

Discussion

Our point here is not that any of these publications is wrong. Rather, we want to highlight the potential for taxonomic errors in publications where the sampling area is very distant from the species' type locality. As pointed out by one of the reviewers, for coastal cephalopod species in complex habitats, such errors are possible even at very small distances. Any taxonomic error introduced by this geographic mismatch may be compounded when the sequence is archived in a genomic database and the database is used for other investigations.

We therefore recommend selection of specimens for genomic sequencing collected from as close to the type locality of the species as possible. Although we recognize that it may not always be possible to sample the type locality, we recommend that the genomic sample be from the same biogeographic province (e.g., GOODS, 2009 or subsequent modifications by various authors) or "Large Marine Ecosystem" (LME – Sherman and Duda, 2011) as the type locality. The collecting locality should always be included in any publication resulting from DNA sequencing. Furthermore, specimens should not be

selected for sequencing from a source where the actual collecting locality cannot be determined confidently (e.g., not from fishery landings, etc.). Also, although our primary purpose here is to highlight the need for sequenced specimens to come from as close to the type locality as possible, we also recommend that specimens sequenced and any unprocessed tissue be vouchered in an established archival collection. Relevant information about archived material (e.g., museum catalogue number) should be included in resulting publications.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Ethics statement

Ethical review and approval was not required for the animal study because this is a literature review. No animals (live or preserved) were used.

Author contributions

MS conceived the idea. MV and MS analyzed the data. PR accumulated the references. MV wrote the first draft. All authors contributed to the final manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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