Spatiotemporal occurrence of summer ichthyoplankton in the southeast Beaufort Sea

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Abstract

Current trends of fish communities in the interior Arctic Ocean are largely unknown, whereas more fishes of boreal origin are reported from the Chukchi and Barents Seas recently. To assess variability in species composition and spatiotemporal occurrence in ichthyoplankton in the southeast Beaufort Sea, we sampled larval and juvenile fish using square-conical nets in the upper water column (< 100 m) from June to September between 2002 and 2011. Gadidae consisting of *Boreogadus saida* and *Arctogadus glacialis* numerically accounted for > 75% of total catches every month. Cottidae and Liparidae usually followed Gadidae, together representing 9–94% of non-gadid species in number. The majority of dominant and subdominant species occurred ubiquitously through the sampling area, whereas *Gymnocanthus tricuspis* (Cottidae), *Liparis gibbus* (Liparidae), and *Leptoclinus maculatus* (Stichaeidae) occurred abundantly on the Mackenzie Shelf. In contrast, *Triglops nybelini* (Cottidae) was frequently found in the Amundsen Gulf, which was characterized by higher salinities (> 25). Exceptional species composition was observed in September 2011, when *Ammodytes hexapterus* (Ammodytidae) numerically accounted for 67% of non-gadid species. In the southeast Beaufort Sea, summer ichthyoplankton are characterized by the overwhelming dominance of Arctic gadids as well as the frequent occurrence of Arctic cottids and liparids. However, the sudden and frequent occurrence of *A. hexapterus* may be a first sign of significant changes in fish communities in the interior Arctic Ocean.

Keywords (4-6 words) *Ammodytes hexapterus* · Arctic Ocean · climate change · fish community · horizontal distribution · Pacific sand lance

Introduction

Sea surface warming combined with increasing river discharge and changing ocean currents will strongly impact the Arctic marine ecosystem within the next half a century (ACIA 2005). Although fish constitute the main energy channel from invertebrates to seabirds, seals, and whales in the Arctic Ocean (Bradstreet and Cross 1982; Welch et al. 1992), fish communities have mostly been studied in the main gateways to the Arctic Ocean, such as the Chukchi Sea (Mecklenburg et al. 2007; Norcross et al. 2010; Lin et al. 2012), Barents Sea (Byrkjedal and Høines 2007; Eriksen et al. 2011, 2012) and Baffin Bay (Munk et al. 2003; Jørgensen et al. 2011). Recently, more fishes of boreal origin occur in these gateways, as many species are extending their distribution ranges northward (Perry et al. 2005; Fleischer et al. 2007; Mueter and Litzow 2008). Given that such biological invasions are threatening fishes of Arctic origin (Christiansen et al. 2014; Falardeau et al. 2014), current trends of fish communities should be investigated not only in the gateways but also in the interior Arctic Ocean, which is not directly influenced by Pacific or Atlantic waters (Carmack and Wassmann 2006).

The southeast Beaufort Sea is characterized by all topographic features that typically characterize the interior Arctic Ocean: large estuarine system, shallow continental shelf, and deep ocean basin (Carmack and Wassmann 2006). The Mackenzie River plume dominates the surface water layer over the Mackenzie Shelf, sometimes extending to the Canada Basin over the Beaufort Slope (Macdonald and Yu 2006). Following the first interdisciplinary study in the 1980s (Northern Environmental Protection Branch 1985), several large-scale research programs have been conducted in this area (Fortier et al. 2008; Barber et al. 2012). These research programs have accumulated baseline information about fish communities in coastal waters (Chiperzak et al. 1990, 2003a, b, c; Majewski et al. 2006, 2009, 2011, 2013) as well as for the dominant fish species, polar cod *Boreogadus saida* (Benoit et al. 2008, 2010; Bouchard and Fortier 2011; Bouchard et al. 2013, in press; Geoffroy et al. 2011; Walkusz et al. 2011, 2012; Falardeau et al. 2014). Recent studies reported that the Mackenzie River plume dictates the distribution of ichthyoplankton communities on the Mackenzie Shelf (Paulic and Papst 2012; Wong et al. 2013). However, little or no information is available concerning subdominant fishes, especially in offshore waters.

As a first step for investigations into current trends of fish communities in the southeast Beaufort Sea, the present study focused on larval and juvenile fish in the upper water column (hereafter, ichthyoplankton). Physical and biological sampling was conducted in summer between 2002 and 2011. We examined (1) interannual changes in species composition and (2) variability in the spatiotemporal occurrence of dominant and subdominant species.

Materials and Methods

Study region

The southeast Beaufort Sea is comprised of the Mackenzie Shelf, the Beaufort Slope, and the Amundsen

Gulf (Fig. 1). The Mackenzie Shelf is a shallow rectangular shelf (520 km × 120 km), bordered by the Mackenzie Trough to the west, the Amundsen Gulf to the east, and the Beaufort Slope to the north (shelf break depth, ca. 100 m). The Mackenzie River, the fourth largest river flowing into the Arctic Ocean, delivers a large amount of fresh water and sediments to the Mackenzie Shelf mainly from May to September (Macdonald and Yu 2006). Three water layers of distinctive origins co-occur in the sea: the Polar Mixed Layer (< 50 m), the Pacific Halocline (50–200 m), and the Atlantic Layer (> 200 m) (Carmack et al. 1989; Macdonald et al. 1989). The Polar Mixed Layer consists of sea ice melt and river discharge as well as Pacific or Atlantic waters that have been mixed sufficiently to have lost their original identity. In summer, changeable wind forcing primarily dictates water movement on the Mackenzie Shelf (Carmack and Macdonald 2002; Williams and Carmack 2008), whereas off the shelf relatively constant currents exist: the Beaufort shelf break jet flowing eastward along the Beaufort Slope and the Beaufort Gyre flowing westward in the southern Canada Basin (Pickart 2004; Steele et al. 2004).

Field sampling

Physical and biological sampling was conducted in the southeast Beaufort Sea from June to September between 2002 and 2011 onboard Canadian Coast Guard icebreakers. Vertical profiles of temperature and salinity were obtained at 1-m intervals with a rosette-type oceanographic profiler equipped with a Seabird CTD. Ichthyoplankton were sampled using a double square-net (DSN) sampler that consisted of a rectangular frame carrying two square-conical nets (1 m^2 opening, 6 m long; Bouchard et al. in press). As ichthyoplankton increased in size during the sampling season, the mesh size was changed from 200 or 500 μm to 750 or 1600 μm. The DSN sampler was towed obliquely in the surface layer (< 100 m) at a speed of ca. 1 m s^{-1}. The maximum sampling depth was determined in accordance with bottom depth at each station. The volume of water filtered was calculated from ship speed and towing duration, due to the frequent failure of flow meters in frigid waters. Biological sampling stations were selected among physical sampling stations in each year. The selected stations were arranged throughout the southeast Beaufort Sea in 2004 and 2008, whereas in 2009 and 2010 they were concentrated around the shelf break (Fig. 1). In addition to oblique tows using the DSN sampler, several water layers were sampled separately using a EZNet multi-layer sampler (2–9 layers; Bouchard et al. in press) to assess the vertical distribution of ichthyoplankton in July 2004. Square-conical nets (1 m^2 opening, 200 or 333 μm mesh) mounted on the EZNet sampler were opened sequentially and towed obliquely at a speed of ca. 1 m s^{-1}. The number and depth of water layers sampled were set in accordance with bottom depth at each station. The volume of water filtered was calculated from a flow meter attached to the EZNet sampler. Ichthyoplankton specimens were enumerated and most were measured for fresh standard length (SL) onboard before individual preservation in 95% ethanol.

Laboratory analysis

All ichthyoplankton specimens were enumerated, identified morphologically to the lowest taxonomic level possible, and measured for preserved standard length. Fresh standard length of individuals not measured at sea was estimated from their preserved standard length using family-specific relationships obtained from individuals measured at sea. The morphological identification was realized following relevant literature (e.g. Able et al. 1986; Matarese et al. 1989; Fahay 2007a, b; Blood and Matarese 2010), whereas scientific names followed Mecklenburg et al. (2011). Families were listed in accordance with Nelson (2006) and species were listed alphabetically within each family. The two gadid species *B. saida* and *Arctogadus glacialis* were pooled in Gadidae because of close similarities in morphology during their early life stages. As genetic (Nelson et al. 2013) and otolithometric (Bouchard et al. 2013) analysis have recently enabled identification of the two gadid species, their respective early life histories have been compared and published elsewhere (Bouchard and Fortier 2011; Bouchard et al. in press). Identification of *Ammodytes hexapterus* was confirmed by genetic analysis (Falardeau et al. 2014).

Results

Both Amundsen Gulf and Beaufort Slope were characterized by consistently higher salinities (> 25) in contrast with variable salinities off the mouth of the Mackenzie River (Fig. 2). The river plume was visible in 2004 with the distribution of higher temperatures and lower salinities in surface waters (> 4ºC and < 25, respectively). The river plume was also observed at least partially in 2008 and 2009, whereas in other years it was not detected within the area observed. Spatial differences in temperature and salinity were less marked in subsurface waters (not shown).

Gadidae numerically accounted for > 75% of monthly catches in each year (Fig. 3). Besides Gadidae, 5 families, 11 genera, and 13 species were identified (Table 1). Cottidae and Liparidae usually followed Gadidae, together representing 9–94% of non-gadid species in number. In Cottidae, *Gymnocanthus tricuspis* and *Triglops nybelini* were the dominant species. *Liparis fabricii* was more abundant than *Liparis gibbus* in Liparidae. Other subdominant species included *Leptoclinus maculatus* (Stichaeidae), *Stichaeus punctatus* (Stichaeidae), *Aspidophoroides olrikii* (Agonidae), and *A. hexapterus* (Ammodytidae). Although *A. hexapterus* larvae and juveniles were caught only in 2010 and 2011, they numerically accounted for 67% of non-gadid species in 2011.

Growth during a prolonged planktonic period was reflected by the increasing SL frequency distributions of *T. nybelini*, *L. fabricii*, *L. gibbus*, and *A. olrikii*, from June to September (Fig. 4). In these species, SL increased from 10 mm in June to > 30 mm in September at an average growth rate of > 0.2 mm day^{-1}. In contrast, early settlement after a shorter planktonic period was suggested in *G. tricuspis* and *S. punctatus* as their occurrence was restricted both in terms of size and season: *G. tricuspis*, < 20 mm SL in July; *S. punctatus*, < 25 mm SL in September. *Leptoclinus maculatus* of various sizes (12–50 mm SL) occurred from June to September, with no clear pattern in its SL frequency distribution. *Ammodytes hexapterus* occurred abundantly only in September 2011 (12–53 mm SL).

The spatial occurrence of dominant and subdominant species was classified into three groups: ubiquitous through the sampling area, abundant on the shelf, and abundant off the shelf (Fig. 5). The ubiquitous distribution was evident in Gadidae and *L. fabricii*, whereas it was less evident in *S. punctatus*, *A. olrikii*, and *A. hexapterus*. Generally, *G. tricuspis*, *L. gibbus*, and *L. maculatus* occurred more abundantly on the Mackenzie Shelf. In contrast, *T. nybelini* occurred more abundantly off the shelf, specifically in the Amundsen Gulf. Whereas peak abundance of most species corresponded with the plankton bloom in June and July (Tremblay et al. 2012), higher densities of *S. punctatus* were observed in September.

In July 2004, the majority of ichthyoplankton were distributed in the Polar Mixed Layer (< 50 m), independent of bottom depth (30–490 m, Online Resource 1). The number of larval and juvenile fish caught by the EZNet sampler was 293 (26 tows), 201 (84 tows), and 10 (54 tows) in depth layers < 10, 10–50, and > 50 m, respectively. Gadidae numerically accounted for > 75% of catches in all depth layers. These results corroborated the validity of the regular sampling method employed in the present study (i.e. oblique tows in the upper water column).

Discussion

Ichthyoplankton in the interior Arctic Ocean

Geographic isolation from Pacific and Atlantic waters, combined with large estuarine system, shallow continental shelf, and deep ocean basin, characterizes the interior Arctic Ocean (i.e. the Beaufort, East Siberian, Laptev, and Kara Seas; Carmack and Wassmann 2006). The fish species composition described here, with an overwhelming dominance of Gadidae, a subdominance of Cottidae and Liparidae of Arctic origin, and frequent occurrence of Agonidae and Stichaeidae, can be considered to be characteristic of summer ichthyoplankton in the interior Arctic Ocean. The two Arctic gadids *B. saida* and *A. glacialis* represented > 75% of the ichthyoplankton in the present study, irrespective of sampling depth or year. Between the two species, *B. saida* have been shown to outnumber *A. glacialis* by a factor of 12 in the southeast Beaufort Sea (Bouchard et al. in press). The two Arctic cottids *G. tricuspis* and *T. nybelini*, and the two Arctic liparids *L. fabricii* and *L. gibbus* frequently occurred in our samples and are likely widespread elsewhere in the interior Arctic Ocean. In contrast with coastal and estuarine waters (Chiperzak et al. 1990, 2003a, b, c; Majewski et al. 2006, 2009, 2011, 2013; Paulic and Papst 2012; Wong et al. 2013), no diadromous or estuarine species, such as Pacific herring *Clupea palasii palasii* and whitefishes *Coregonus* spp., were found in our study area. Fish species composition similar to ours was reported from the adjacent southwest Beaufort and Chukchi Seas, although in these seas fishes of Arctic origin are occasionally replaced by fishes of boreal origin, including capelin *Mallotus villosus*, yellowfin sole *Limanda aspera*, or Bering flounder *Hippoglossoides robustus* (Jarvela and Thorsteinson 1999; Norcross et al. 2010; Lin et al. 2012). On the other hand, an overwhelming dominance of fishes of boreal origin, such as sand lance *Ammodytes* spp., Atlantic herring *Clupea herengus*, and Atlantic cod *Gadus* *morhua*, was reported for ichthyoplankton in the Barents Sea and Baffin Bay (Munk et al. 2003; Eriksen et al. 2011, 2012).

Potential effects of climate change on Arctic ichthyoplankton

Although the spatiotemporal resolution of our sampling was not sufficient to correlate ichthyoplankton densities to environmental parameters, some general patterns of spatial occurrence can nonetheless be drawn. For example, *G. tricuspis*, *L. gibbus*, and *L. maculatus* occurred abundantly on the Mackenzie Shelf, indicating early life histories associated with shallow waters, where the river plume frequently brings higher temperatures and lower salinities in summer. Whereas *T. nybelini* occurred abundantly in the Amundsen Gulf, many other species were found ubiquitously through the southeast Beaufort Sea. In temporal patterns, the majority of dominant and subdominant species exhibited gradual growth during a longer planktonic period, although early settlement after a shorter planktonic period was suggested in *G. tricuspis* and *S. punctatus* as their occurrence was restricted both in terms of size and season (Brown and Green 1976).

In the interior Arctic Ocean, ichthyoplankton species would be impacted by ongoing climate change differently in response to their respective early life histories. Shelf-associated species are more vulnerable to changes in river discharge, whereas variability in water temperature and ocean currents is more likely to affect species with an extended planktonic period (cf. ACIA 2005). Besides such direct impacts, environmental changes could affect Arctic ichthyoplankton indirectly through trophic relationships. Sea ice retreat will likely increase light availability and wind-driven upwelling to enhance phytoplankton production over continental shelves, whereas in ocean basins sea surface freshening and warming probably strengthen stratification and prevent the replenishment of nutrients available for phytoplankton (Carmack and McLaughlin 2011; Tremblay et al. 2012). According to this scenario, consumers might benefit from bottom-up effects of increasing phytoplankton production only on continental shelves. Such spatial heterogeneity should be addressed in further investigations into Arctic ichthyoplankton relative to their changing environment.

Ichthyoplankton diversity and abundance can serve as an indicator of changing ocean conditions (e.g. Brodeur et al. 2008). The high abundance of *L. maculatus* in June 2008 and of *A. hexapterus* in September 2011 represents significant invasions of fishes of boreal origin in our study area. The substantial presence of these species, rarely found in ichthyoplankton in the southeast Beaufort Sea (Chiperzak et al. 1990, 2003a, b, c; Paulic and Papst 2012; Wong et al. 2013), most likely results from recent environmental changes in this area (e.g. sea surface warming and sea ice loss; Wood et al. 2013). Although there is a possibility of aberrant drift from the northern Bering Sea (Berline et al. 2008), significant reproduction of *A. hexapterus* in the Beaufort Sea in 2011 is strongly suggested by its unimodal size/age frequency distributions including small/young individuals (< 20 mm SL or < 10 days old; Falardeau et al. 2014). A similar inference about *L. maculatus* can be drawn from its SL frequency distribution (cf. Meyer Ottesen 2011). As such, ichthyoplankton may act as sentinels of climate change, detecting significant reproduction of new species and forecasting biological invasions in a given area. Moreover, ichthyoplankton species observed in the present study have a benthic (12 species) or bentho-pelagic (*B. saida*, *A. glacialis*, and *A. hexapterus*) adult stage, and therefore characterized by different vulnerability to standard fishing gear such as bottom or pelagic trawls during the adult stage. Intense bottom trawl surveys conducted on certain Arctic shelves also bring concerns about habitat destruction (Christiansen et al. 2014). Ichthyoplankton surveys thus constitute a powerful tool to assess the response of fish communities to environmental changes in the interior Arctic Ocean.

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Table 1 Summary of ichthyoplankton caught by a double square-net sampler in the southeast Beaufort Sea in summer between 2002 and 2011. Gadidae spp. consist of *Boreogadus saida* and *Arctogadus glacialis*

Year	2002	2004				2005	2008		2009		2010	2011
Month	Sep	Jun	Jul	Aug	Sep	Sep	Jun	Jul	Jul	Aug	Aug	Sep
Day	23–30	9–28	2–31	1–10	6–13	2–13	2–30	1–31	18–27	4–21	15–25	8–30
Number of tows	17	17	34	8	23	8	9	17	19	8	18	22
Number of individuals caught	301	531	1497	170	134	22	625	545	1967	907	411	774
Mean density (1000 m^{-3})	10	94	124	29	9	5	131	81	178	215	28	41
Maximum density (1000 m^{-3})												
Gadidae												
Gadidae spp.	33	302	1100	104	53	17	471	645	1615	906	97	90
Cottidae												
Gymnocanthus tricuspis	0	0	171	2	0	0	0	136	6	3	2	0
Icelus bicornis	0	0	3	0	0	0	21	0	0	0	0	0
Myoxocephalus quadricornis	0	0	3	0	0	0	0	0	0	0	0	0
Triglops nybelini	0	36	7	3	2	0	2	17	2	0	1	1
Triglops pingeli	0	0	0	0	0	0	3	0	0	0	0	1
Agonidae												
Aspidophoroides olrikii	0	2	3	0	4	2	3	4	4	1	2	1
Leptagonus decagonus	0	0	0	0	0	0	0	0	0	0	0	1
Liparidae												
Liparis fabricii	2	25	30	3	8	1	7	10	20	4	9	2
Liparis gibbus	0	0	2	0	1	0	12	0	44	0	5	1
Stichaeidae												
Leptoclinus maculatus	0	2	8	0	14	0	82	2	0	0	0	1
Lumpenus lampretaeformis	0	0	0	0	0	0	0	0	0	1	0	0
Stichaeus punctatus	0	0	0	1	0	0	0	9	0	0	1	7
Ammodytidae												
Ammodytes hexapterus	0	0	0	0	0	0	0	0	0	0	3	29

Figure Captions

Fig. 1 Sampling stations for the double square-net sampler in the southeast Beaufort Sea in summer between 2002 and 2011. Continental shelves (< 100 m) are shaded

Fig. 2 Sea surface temperature (a) and salinity (b) observed in the southeast Beaufort Sea in the summers of 2004, 2008, 2009, and 2011. Small dots represent locations where CTD casts were conducted. The isobathic lines indicate 100 m in depth

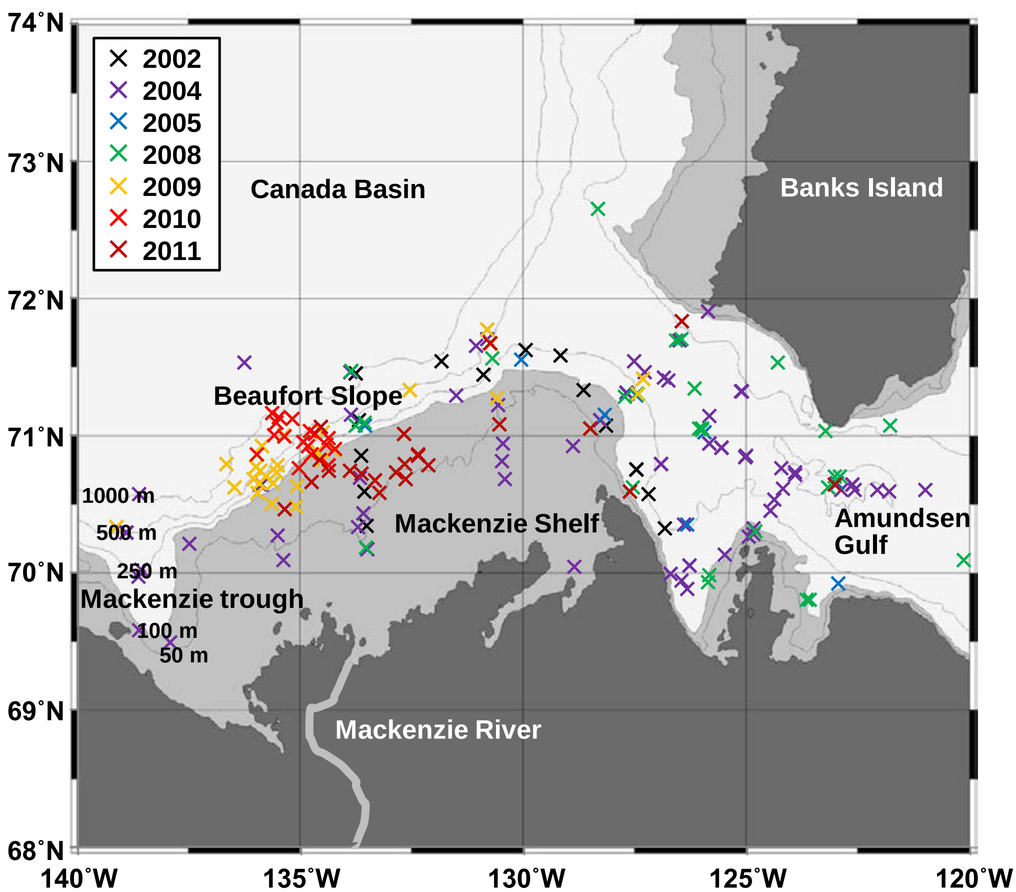
Fig. 3 Numerical composition of ichthyoplankton caught by the double square-net sampler in the southeast Beaufort Sea in summer between 2002 and 2011. Gadidae consisting of *Boreogadus saida* and *Arctogadus glacialis* are contrasted with other families in (a); all species except Gadidae are shown in (b)

Fig. 4 Length frequency distributions of subdominant ichthyoplankton species caught by the double square-net sampler in the southeast Beaufort Sea in summer between 2002 and 2011 (pooled years). Sampling months are indicated with a gray scale

Fig. 5 Spatial occurrence of dominant and subdominant ichthyoplankton species caught by the double square-net sampler in the southeast Beaufort Sea in summer between 2002 and 2011 (pooled years). Monthly occurrence is shown for Gadidae (a), Cottidae (b), Liparidae (c), Stichaeidae (d), and others (e). Gadidae consists of *Boreogadus saida* and *Arctogadus glacialis*. Note that the scale of density may differ among plots

Online Resource 1 Sampling stations for the EZNet sampler in the southeast Beaufort Sea in July 2004 (a), vertical distribution of ichthyoplankton relative to the bottom depth at each sampling station (b), and numerical composition of ichthyoplankton caught by the EZNet sampler at different depth layers (c). Gadidae consists of *Boreogadus saida* and *Arctogadus glacialis*

Fig. 1



2002
2004
2005
2008
2009
2010
2011
Canada Basin
Banks Island
Beaufort Slope
Mackenzie Shelf
Amundsen Gulf
Mackenzie trough
Mackenzie River
1000 m
500 m
250 m
100 m
50 m
74˚N
73˚N
72˚N
71˚N
70˚N
69˚N
68˚N
140˚W
135˚W
130˚W
125˚W
120˚W

Fig. 2

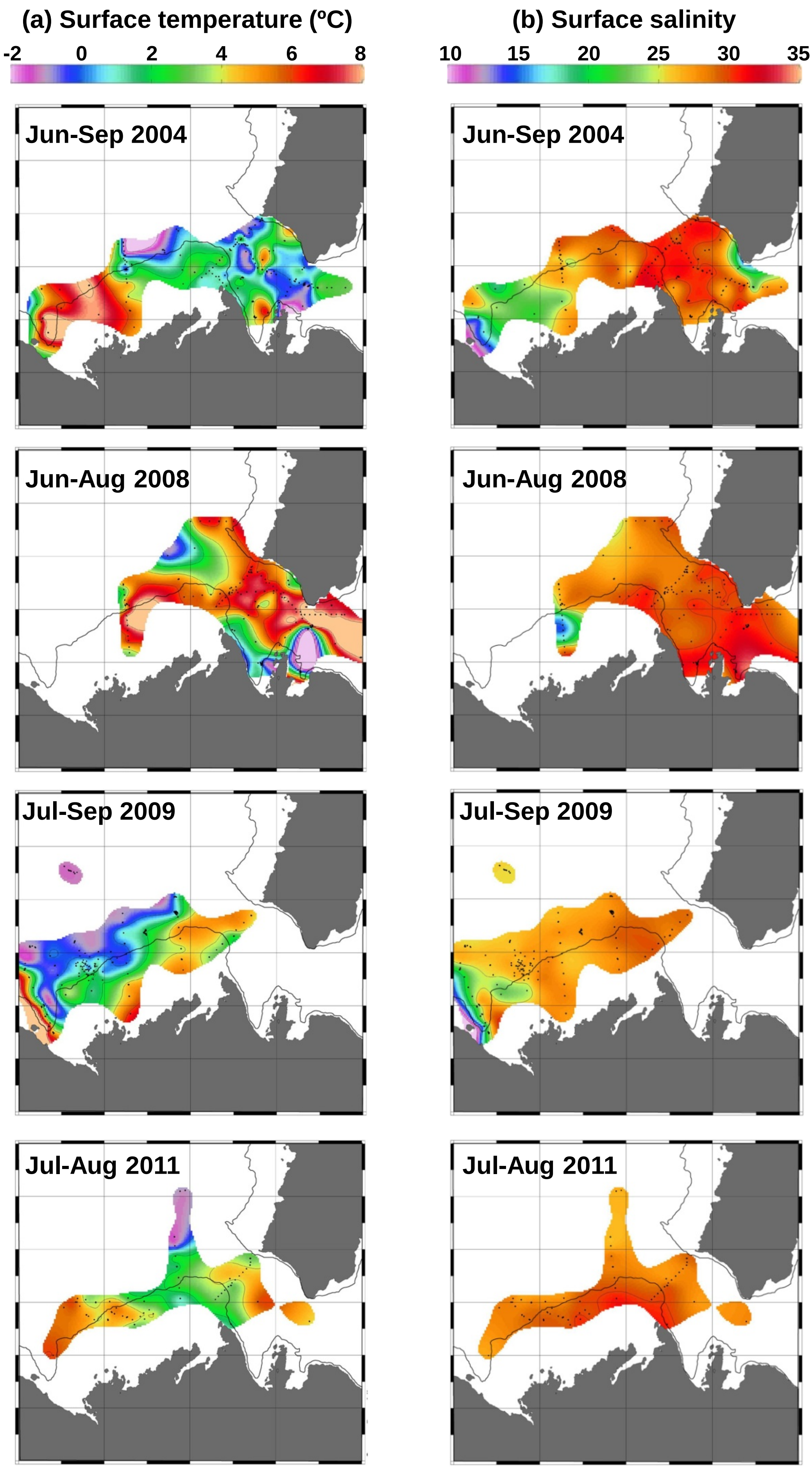

(a) Surface temperature (ºC)
-2
0
2
4
6
8
(b) Surface salinity
10
15
20
25
30
35
Jun-Sep 2004
Jun-Sep 2004
Jun-Aug 2008
Jun-Aug 2008
Jul-Sep 2009
Jul-Sep 2009
Jul-Aug 2011
Jul-Aug 2011

Fig. 3

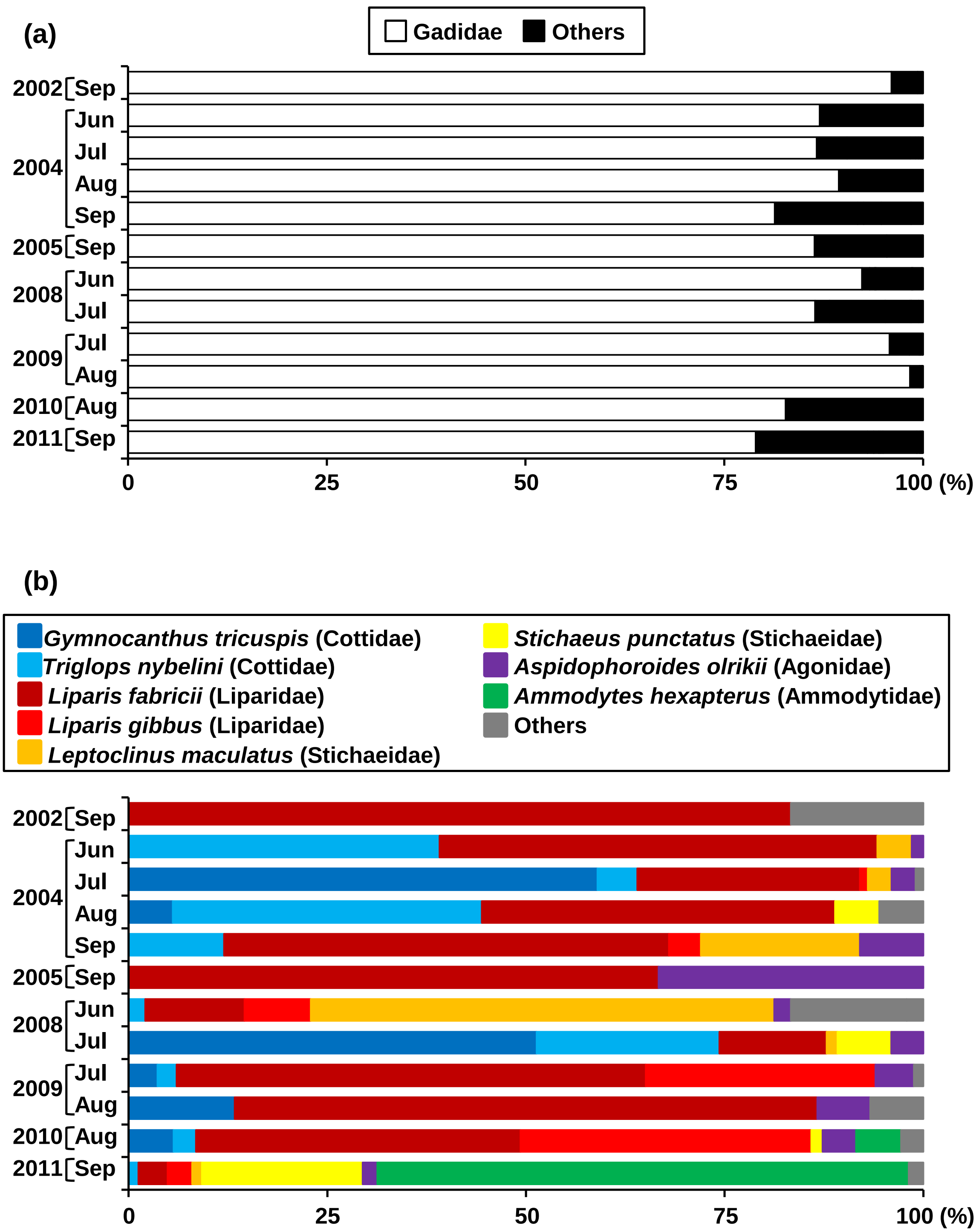

(a)
Gadidae
Others
2002 Sep
2004 Jun
Jul
Aug
Sep
2005 Sep
2008 Jun
Jul
2009 Jul
Aug
2010 Aug
2011 Sep
0
25
50
75
100 (%)
(b)
Gymnocanthus tricuspis (Cottidae)
Triglops nybelini (Cottidae)
Liparis fabricii (Liparidae)
Liparis gibbus (Liparidae)
Leptoclinus maculatus (Stichaeidae)
Stichaeus punctatus (Stichaeidae)
Aspidophoroides olrikii (Agonidae)
Ammodytes hexapterus (Ammodytidae)
Others
2002 Sep
2004 Jun
Jul
Aug
Sep
2005 Sep
2008 Jun
Jul
2009 Jul
Aug
2010 Aug
2011 Sep
0
25
50
75
100 (%)

Fig. 4

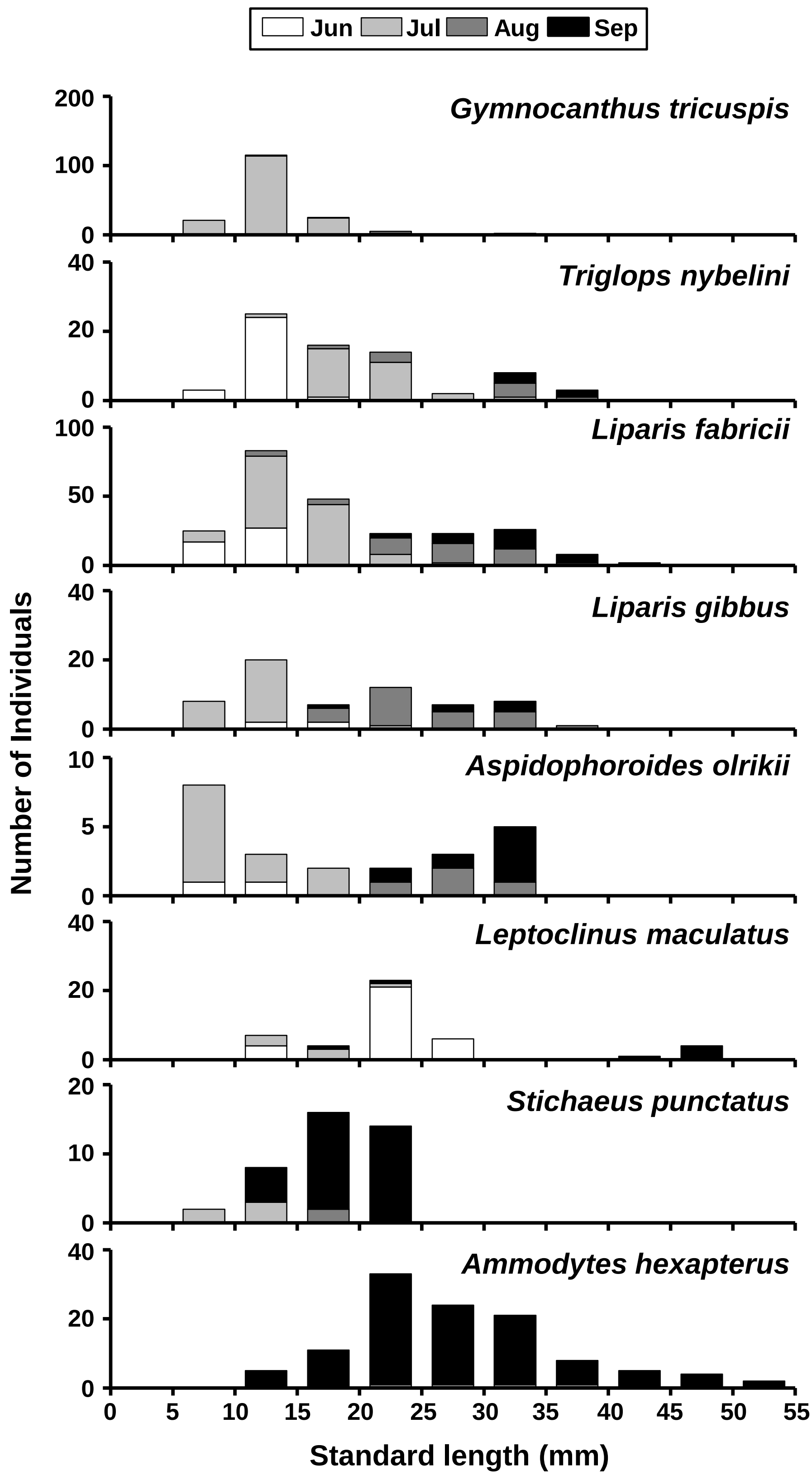
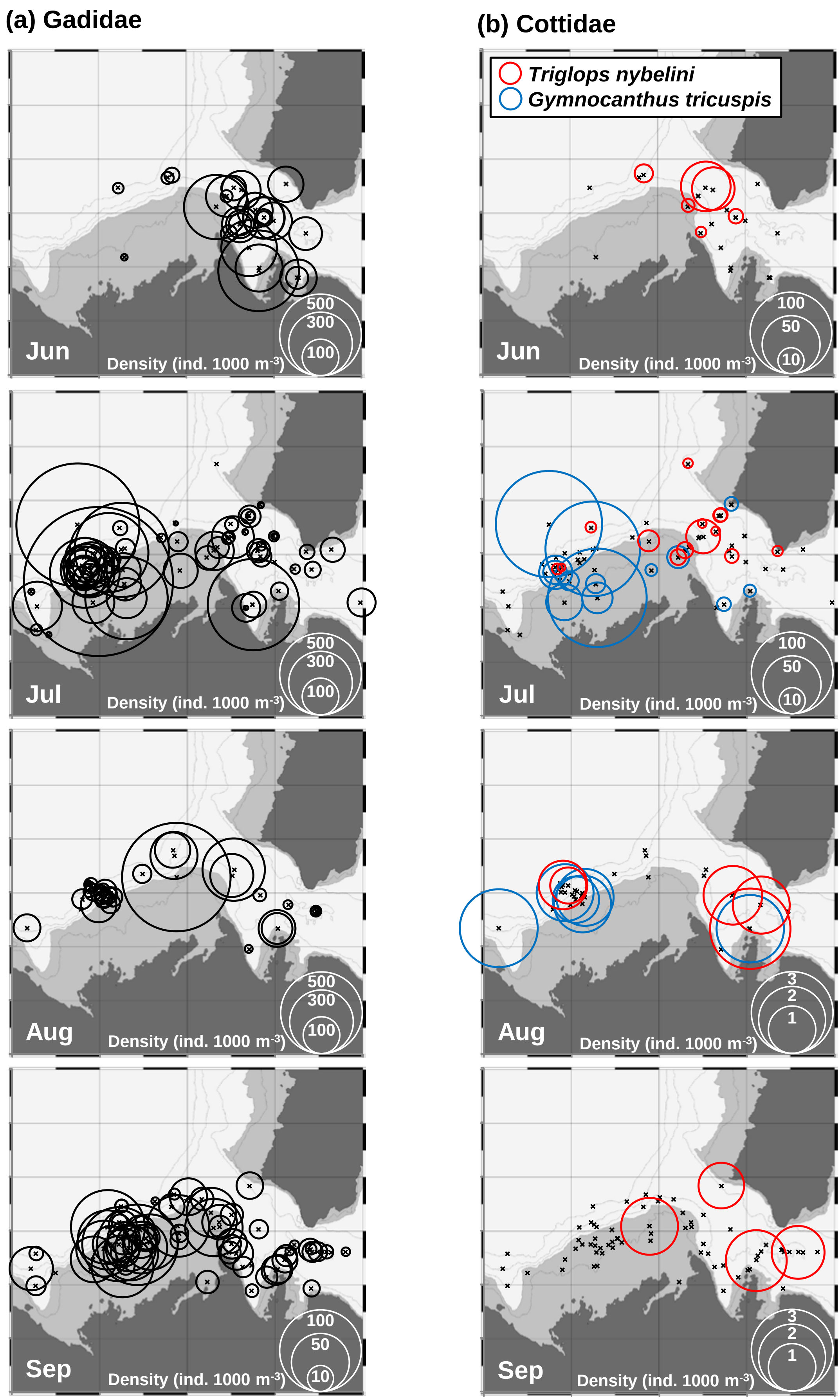

Jun
Jul
Aug
Sep
Gymnocanthus tricuspis
Triglops nybelini
Liparis fabricii
Liparis gibbus
Aspidophoroides olrikii
Leptoclinus maculatus
Stichaeus punctatus
Ammodytes hexapterus
Number of Individuals
Standard length (mm)
0
5
10
15
20
25
30
35
40
45
50
55
100
200
50
40

Fig. 5



(a) Gadidae
(b) Cottidae
Triglops nybelini
Gymnocanthus tricuspis
Jun
Jul
Aug
Sep
Density (ind. 1000 m-3)
500
300
100
50
10
3
2
1

Fig. 5 (continued)

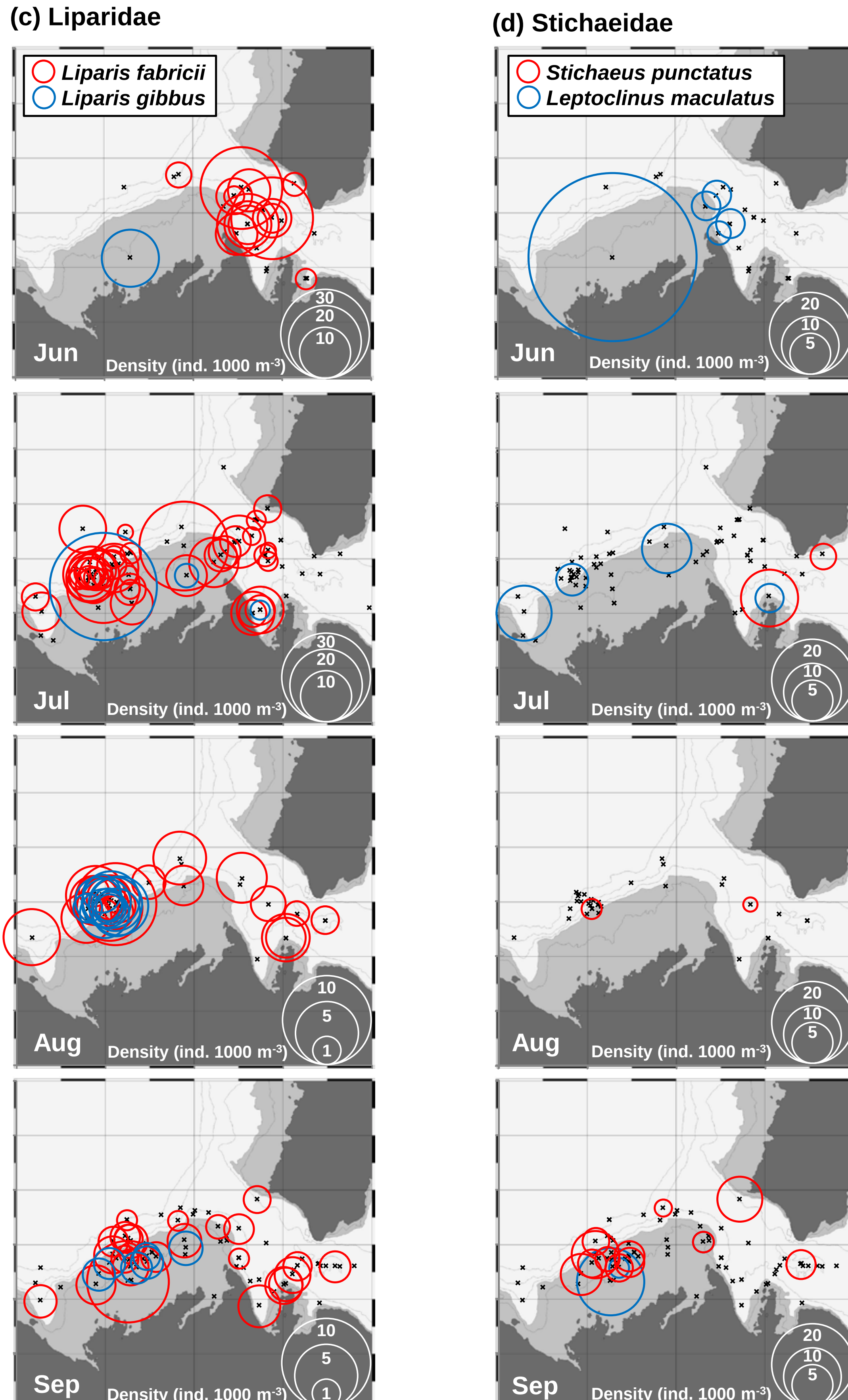
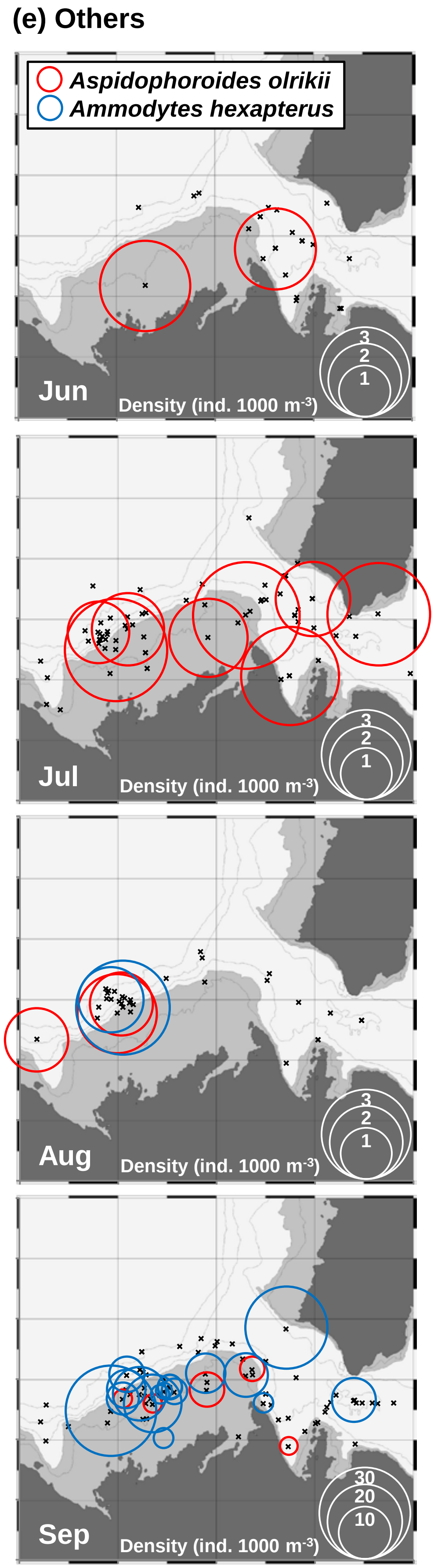


Fig. 5 (continued)



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Online Resource 1 Sampling stations for the EZNet sampler in the southeast Beaufort Sea in July 2004 (a), vertical distribution of ichthyoplankton relative to the bottom depth at each sampling station (b), and numerical composition of ichthyoplankton caught by the EZNet sampler at different depth layers (c). Gadidae consists of *Boreogadus saida* and *Arctogadus glacialis*