UNIVERSITY OF NOVA GORICA
SCHOOL OF ENVIRONMENTAL SCIENCES

PTEROPODS IN THE WORLD ATLAS OF MARINE PLANKTON FUNCTIONAL TYPES

DIPLOMA THESIS

Jasna MOŽINA

Supervisor: dr. Nina Bednaršek

Nova Gorica, 2013

DECLARATION

The work presented in this bachelor thesis is the result of the original research work of the author. The results in this thesis, either obtained in collaboration with other researches or contributed by the researches (experts) themselves are marked explicitly and cited accordingly.

IZJAVA

Izjavljam, da je diplomsko delo rezultat lastnega raziskovalnega dela. Rezultati, ki so nastali v okviru skupnega raziskovanja z drugimi raziskovalci, ali so jih prispevali drugi raziskovalci (strokovnjaki), so eksplicitno prikazani oziroma navedeni (citirani) v diplomskem delu.

Jasna Možina

Acknowledgements

Many thanks go to my mentor and supervisor Dr. Nina Bednaršek for all the help, assistance and guidance during the research and writing of this diploma thesis. Sincere thanks also to my parents and my friends who supported me and stood by my side during my studies.

Zahvala

Zahvaljujem se svoji mentorici, Dr. Nini Bednaršek, za vso pomoč, usmerjanje in vodenje pri raziskovalnem delu in pisanju diplomskega dela. Resnično velik hvala tudi mojim staršem in mojim prijateljem, ki so me podpirali in mi stali ob strani ves čas mojega študija.

Summary

Pteropods are marine holoplanktonic molluscs that are widely distributed across world oceans and are recently in the spotlight of research due to their vulnerability to global ocean changes, such as ocean acidification, warming and deoxygenation. They play an important ecological and biochemical role in marine ecosystems, this making them one of several important plankton functional types. Based on their functionality, they are to be included into models of marine ecosystems and biogeochemical cycles, which requires sufficient amount of data to be collected prior incorporating a group into the model. With the aim of becoming a valuable model validation tool, the first global database of pteropod carbon biomass was thus created under the MARine Ecosystem Data (MAREDAT) initiative - a collective effort of scientists to create a global marine atlas of important plankton functional types. Data analysis provided an overview of the pteropod distribution on the temporal and spatial (latitudinal and vertical) scale. Biomass concentration of pteropods was the highest at the poles and generally decreased towards equator, while vertical distribution peaked at the surface 0-10 m and gradually decreased with depth. The global calculated mean and median biomass concentrations were 4.6 mg C m^{-3} (std= 62.5) and 0.015 mg C m^{-3}, respectively with annual carbon production of 444-505 Tg C yr^{-1}. Mean global carbonate biomass of thecosomes was 23.17 mg $CaCO_3$ m^{-3} with annual aragonite production of 829-943 Tg $CaCO_3$ yr^{-1}.

Key Words: pteropods, carbon biomass, aragonite shell, ocean acidification, biogeochemical models

Povzetek

Pteropodi so majhni morski holoplanktonski mehkužci razširjeni v svetovnih oceanih. Zakisljevanje, segrevanje in deoksigenacija morja, kot posledice globalnih klimatskih sprememb, naj bi bistveno vplivale na pteropode, ki so zato postali fokus raziskav. Ker lahko v morskih ekosistemih igrajo pomembno ekološko in biogeokemijsko vlogo, so bili prepoznani kot ena izmed funkcionalnih planktonskih skupin, ki jih je pomembno vključevati v modele, ki simulirajo funkcioniranje morskih ekosistemov in biogeokemijske cikle. Pogoj za slednje je zadostna količina podatkov o pteropodih. Z namenom uporabe podatkov za sestavo in preverjanje modelov, je bila ustvarjena prva baza s podatki o globalni ogljikovi biomasi pteropodov, kot del mednarodne iniciative MARine Ecosystem DATa (MAREDAT). Namen slednje je ustvariti svetovni atlas pomembnih planktonskih funkcionalnih tipov. Rezultati analize podatkov o biomasi pteropodov so prikazali porazdelitev zbiranja podatkov biomase v časovnem in prostorskem okviru ter globalno geografsko, vertikalno in sezonsko razširjenost biomase pteropodov. Biomasa pteropodov je bila najvišja na polih in je splošno padala proti ekvatorju, vertikalno pa so bile najvišje biomase izmerjene med 0-10 m in so padale z globino. Povprečna izračunana globalna ogljikova biomasa pteropodov je bila 6 mg C m^{-3} (std= 62,5), z mediano 0,015 mg C m^{-3} in letno globalno produkcijo ogljika 444-505 Tg C $leto^{-1}$. Globalna karbonatna biomasa pteropodov z aragonitnimi lupinami je bila 23,17 mg $CaCO_3$ m^{-3}, letna produkcija karbonata pa 829-943 Tg $CaCO_3$ $leto^{-1}$.

Ključne besede: pteropodi, ogljikova biomasa, aragonitna lupina, zakisljevanje morja, biogeokemijski modeli

Obsežnejši povzetek v slovenščini

Pteropodi v svetovnem atlasu morskih planktonskih funkcionalnih tipov

Diplomsko delo

1 UVOD

1.1 Splošni uvod

Posledica človekovih dejavnosti, pri katerih se v ozračje sproščajo velike količine ogljikovega dioksida (CO_2), so klimatske spremembe ter globalno segrevanje planeta (Sabine C.L. in sod., 2004; IPCC, 2007; Gruber N., 2011). V svetovnih oceanih se skladišči velik delež odvečne toplote, poleg tega pa oceani absorbirajo tudi CO_2 iz ozračja, kar skupaj zaustavlja hitrost klimatskih sprememb (Sabine C.L. in sod., 2004; IPCC, 2007; Sabine C.L. in Feely R.A., 2007). Zaradi konstantnega zviševanja koncentracije CO_2 v ozračju prihaja do sprememb v kemiji morskega okolja - nižanja pH-ja, višanja parcialnega tlaka CO_2 ter posledično nižanja koncentracije karbonatnih ionov v vodi (Feely R.A. in sod., 2004; Orr in sod., 2005; Fabry V.J. in sod., 2008; Widdicombe S. in Spicer J.I., 2008). Te spremembe bodo po pričakovanjih imele velik (negativen) učinek na morske organizme, posebno na planktonske organizme, ki tvorijo karbonatne lupine ali skelete - pteropode, foraminifere, kokolitoforide (Fabry V.J. e tal., 2008; Doney S.C. in sod., 2009). Ti organizmi so del biološke karbonatne črpalke v oceanih, s pomočjo katere se ogljik iz ozračja skladišči v globinah oceanov (Fabry V.J., 1989; Fabry in sod., 2008; Doney S.C. in sod., 2009). Napovedovanje vpliva hkratnega delovanja treh glavnih okoljskih dejavnikov, ki so posledica klimatskih sprememb – segrevanja, zakisljevanja in deoksigenacije oceanov, je izjemno kompleksno. Čeprav znanstvena stroka družno napoveduje spremembe v morskem okolju, si ni edina v tem, kolikšne in kakšne spremembe v biodiverziteti in delovanju morskih ekosistemov ter biogeokemijskih ciklov, kot je na primer črpalka ogljika, lahko pričakujemo (Pörtner H.-O. 2008, 2010; Hoffman G.E. in Todgham A.E., 2010; Byrne M., 2011; Gruber N., 2011; Pinsonneault A.J. in sod., 2012).

Za učinkovito napovedovanje posledic klimatskih sprememb so uporabno orodje modeli, ki simulirajo delovanje morskih ekosistemov in biogeokemijskih procesov (Le Quéré C. in sod. 2005, 2009; Hood R.R. in sod., 2006). Nova generacija biogeokemijskih modelov, imenovanih Dinamični Zeleni Oceanski Modeli (Dynamic Green Ocean Models), vključuje tudi delovanje planktonskih funkcionalnih skupin, ki igrajo pomembne vloge v biogeokemijskih ciklih v morskem okolju (Le Quéré C. in sod., 2005, 2009; Hood R.R. in sod., 2006). Pogoj za reprezentativno prikazovanje vloge funkcionalnih planktonskih skupin v modelih je prvenstveno zadostna količina podatkov o organizmih, ki sestavljajo posamezno skupino. V nasprotnem primeru se zanesljivost modelov, z vnosom dodatnih faktorjev, le manjša (Hood R.R. in sod., 2006). Dostopnost eksperimentalnih podatkov in podatkov opazovalnih študij za funkcionalne planktonske skupine, ki predstavljajo del črpalke ogljika iz površja oceanov v globine, kot so npr. pteropodi, trenutno predstavlja oviro za njihovo vključevanje v modele (Hood R.R. in sod., 2006).

1.2 Namen in cilji

Splošni namen tega diplomskega dela se ujema s cilji mednarodne iniciative MERADAT, pod okriljem projekta MAREMIP (Marine Ecosystem Model Inter-comparison Project). MAREMIP promovira razvoj modelov, ki vključujejo planktonske funkcionalne skupine. Projekt stremi k vzpostavitvi svetovnega atlasa morskih funkcionalnih tipov MARineEcosystem DATa-base (MAREDAT), ki naj bi vsebovala trenutno dosegljive podatke o gostoti in biomasi pomembnih funkcionalnih planktonskih tipov. Eden izmed teh tipov so tudi pteropodi. Cilj raziskovalnega dela diplomske naloge je bil ustvariti podatkovno bazo o globalni biomasi pteoropodov, ki bi bila uporabna kot orodje za sestavljanje in preverjanje modelov, ki simulirajo delovanje morskih ekosistemov in biogeokemijskih procesov v oceanih. Poleg tega je bil namen s pomočjo statistične analize zbranih podatkov meritev gostote/biomase pteropodov, pridobiti rezultate o globalni biomasi, razporeditvi biomase pteropodov v svetovnih oceanih in podatke o doprinosu pteropodov k svetovni produkciji ogljika ter karbonata. Glavni cilj je bil predstaviti rezultate analiz v obliki strokovne publikacije v znanstveni reviji Earth System Science Data (ESSD).

Dodaten cilj tega diplomskega dela je bil tudi pregled znanih podatkov o fiziologiji pteropodov, ki so zelo raznolika skupina živali, kar posledično pomeni raznolike fizične lastnosti, prilagoditve, omejitve in torej tudi odzive na okoljske dejavnike. Poznavanje slednjega je pomembno pri napovedovanju posledic zakisljevanja, deoksigenacije in segrevanja oceanov za pteropode. Namen je bil zbrati tudi podatke o biologiji pteropodov v obliki podatkovne baze, ki predstavlja pomemben vir informacij, uporabnih za modeliranje.

2 TEORETIČNE OSNOVE

2.1 Opis pteropodov

Pteropodi so skupina morskih planktonskih polžkov zaškrgarjev, ki jo sestavljajo polžki brez lupine iz reda Gymnosomata (veslonožci) in polžki iz reda Thecosomata (tekosomati) (Sket B. in sod., 2003). Slednji se deli na dva podredova. V podred Euthecosomata spadajo polžki s karbonatno (aragonitno) lupino, v podred Pseudothecosomata pa polžki brez lupine (Lalli C.M. in Gilmer R.W., 1989). Pteropodi plavajo s pomočjo krilom podobnih parapodnih izrastkov, ki so se razvili iz gastropodne noge (Lalli C.M. in Gilmer R.W., 1989). Pteropodi iz reda Thecosomata so omnivori in hrano lovijo s pomočjo mukusnih mrež, ki jih osebki razpnejo v vodnem stolpcu nad seboj (Gilmer R.W. 1972, 1990; Gilmer R.W. in Harbison G.R, 1986). Prehrana tekosomatov je odvisna od njihove velikosti in od dostopnosti določenega vira hrane (Gilmer R.W. in Harbison G.R, 1991; Gannefors C. in sod., 2005). Veslonožci so specializirani plenilci tekosomatov (Lalli C.M. and Gilmer R.W., 1989; Seibel B.A. in Dierssen H.M., 2003; Seibel B.A. in sod., 2007). Ker so tako odvisni od enega samega vira hrane, so veslonožci razvili prilagoditve za uspešno preživetje dolgih obdobij stradanja (Böer M. in sod. 2005, 2007). Večina pteropodov se sprva razvije v samce ter kasneje v samice, medtem ko lahko veslonožci funkcionirajo kot simultani hermafroditi (Lalli C.M. in Gilmer R.W., 1989; Hunt B.P.V. in sod., 2008). Odrasle samice proizvajajo jajčeca najpogosteje spomladi in poleti, v času ugodnih življenjskih pogojev (npr. visoke primarne produkcije) (Kobayashi H.A., 1974; Wells F.E., 1976; Lalli C.M. in Gilmer R.W., 1989; Dadon J.R. in de Cidre L.L., 1992; Gannefors C. in sod., 2005). Nekatere vrste se razmnožujejo tudi dvakrat ali večkrat v enem letu (Almogi-Labin A. in

sod., 1988; Dadon J.R. in de Cidre L.L., 1992). Predvidevanja o življenjski dobi pteropodov so različna, večinoma med 1 in 3 < let (Kobayashi H.A., 1974; Böer M. in sod., 2005; Gannefors C. in sod., 2005; Bednaršek N. in sod., 2012a). Večina vrst pteropodov je epipelaških, vendar živijo in se zadržujejo tudi v večjih globinah, pod 1000 m (Van der Spoel S., 1967; Wormuth J.H., 1981; Lalli C.M. in Gilmer R.W., 1989; Hunt B.P.V. in sod., 2008). Mnogo vrst pteropodov dnevno ali sezonsko vertikalno migrira iz večjih globin bližje k površju - nekateri dnevno naredijo več kot 350 m globinske razlike (Stepien J.C., 1980; Wormuth J.H., 1981). V tropskih in subtropskih območjih je najti največjo vrstno raznolikost pteropodov, medtem ko se pteropodi najbolj množično pojavljajo v polarnih in sub-polarnih regijah (Lalli C.M. in Gilmer R.W., 1989; Fabry V.J. in sod., 2008).

2.2 Odzivi pteropodov na okoljske dejavnike

Na življenjske vzorce pteropodov vplivajo različni okoljski dejavniki - biotski dejavniki (nihanja v obilju prehrane in pritiski plenilcev) in abiotski dejavniki (temperatura, pritisk, svetloba in turbidnost vode, pH, koncentracija kisika in ogljikovega dioksida). Pteropodi so prilagojeni na različne razmere, specifične za njihovo življenjsko okolje; vrste, ki dnevno migrirajo skozi velik razpon globin, tolerirajo tudi večji razpon abiotskih dejavnikov (Smith K.L. Jr. in Teal J.M., 1973; Wormuth J.H., 1981; Maas A.E. in sod., 2012b). Nasprotno imajo vrste živeče v polarnih ekosistemih nizko toleranco za spreminjanje ekstremnih življenskih pogojev, na katere so zelo specifično prilagojene (Rosenthal J.J.C. in sod., 2008).

Vertikalne migracije pteropodov so način izogibanja plenilcem, povezane tudi s sezonsko večjo primarno produkcijo blizu površja (Mileikovsky S.A., 1970; Falk-Petersen S. in sod., 2008). Od koncentracije in kvalitete hrane je odvisna metabolna aktivnost pteropodov, zato lahko pomanjkanje hrane upočasni njihov razvoj in razmnoževanje, rezultat obilja hrane pa je rast populacije pteropodov (Perissinotto R., 1992; Seibel B.A. in Dierssen H.M., 2003; Bernard K.S., 2006; Böer M. in sod., 2006; Bernard K.S. and Froneman P.W., 2009; Maas A.E. in sod., 2011).

Pteropodi imajo, podobno kot mnogi drugi morski živalski organizmi, svojo temperaturno nišo, znotraj katere vzdržujejo optimalno stopnjo metabolizma, ki je višja pri višjih temperaturah (Pörtner H.-O. 2001, 2008; Seibel B.A. in sod., 2007; Maas A.E. in sod., 2012b). Temperaturna niša določa tudi geografski in vertikalni razpon razširjenosti živali (Pörtner H.-O. 2001, 2002). Visoka temperatura izven temperaturne niše ima lahko dolgoročno negativen učinek na žival, ker je žival nezmožna iz okolja pridobiti zadostne količine kisika, za svoje večje potrebe po energiji pri višji temperaturi (Pörtner H.-O., 2001). Pod vplivom nižanja temperature in koncentracije kisika v okolju pride do nižanja stopnje metabolizma pteropodov (Christou E.D. in sod. in Moraitou-Apostolopoulou M., 1995; Comeau S. in sod., 2010a; Seibel B.A., 2011). Prenizka koncentracija kisika v okolju predstavlja stres za organizem živali, zato je vertikalna razširjenost živali lahko omejena le na s kisikom bogata območja (Maas A.E. in sod., 2012b). Do mešanih metabolnih odzivov pteropodov je prišlo v okolju s povišanimi koncentracijami CO_2, kjer je bilo zabeleženo tako zvišanje kot znižanje stopnje njihovega metabolizma (Maas A.E. in sod. 2012a; Seibel B.A. in sod., 2012). Visoka koncentracija CO_2 lahko povzroči stres v organizmu živali, saj večji vnos CO_2 v telo lahko zmanjša sposobnosti organizma za dovajanje in prenos kisika po telesu (Fabry V.J. in sod., 2008; Pörtner H.-O. 2008, 2010).

Fizikalni dejavniki kot so vetrovi in posledične turbulence v zgornjih plasteh vodnega stolpca, lahko vplivajo na vertikalno razširjenost pteropodov (Tsurumi M. in sod., 2005). Morski tokovi in sezonske hidrografske spremembe (npr. monsuni, ciklonski vrtinci), zaradi katerih pride v okolju do sprememb v temperaturi in koncentraciji nutrientov, vplivajo na geografsko razširjenost ter gostoto populacij pteropodov (Redfield A.C., 1939; Schalk P.H., 1990; Ashjian C.J. in sod., 2001; Mackas D.L. in Galbraith M.D., 2002).

Rast tekosomatov je povezana s kalcifikacijo lupine, ki dokumentirano upada z nižanjem nasičenja vode z aragonitom (Fabry V.J., 1989; Schalk P.H., 1990; Comeau S. in sod. 2009, 2010a; Lischka S. in sod., 2011). Optimalni pogoji za kalcifikacijo so vrstno specifični (Silverman J. in sod., 2007). Če vodno okolje ni nasičeno z aragonitom, pride do raztapljanja ter posledičnih poškodb na lupinah pteropodov (Feely R.A. in sod., 2004; Orr C. in sod., 2005; Bednaršek N. in sod., 2012b), motenj v razvoju lupine pri larvah pteropodov ali celo popolne odsotnosti lupine pri larvah (Comeau S. in sod. 2010a, 2010b; Lischka S. in sod. 2011).

2.3 Funkcija pteropodov v morskih ekosistemih

Pteropodi predstavljajo pomemben del prehranjevalnih verig, posebno v polarnih območjih, kjer lahko dosežejo visoke gostote in tako predstavljajo velik delež celotne populacije zooplanktona teh območij (Ward in sod. P., 2003; Pakhomov E.A. in Froneman P.W., 2004; Pane L. in sod., 2004; Hunt B.P.V. in sod., 2008). Populacije pteropodov učinkovito konzumirajo fitoplankton v času cvetenja in tako pomembno prispevajo k celotni konzumaciji fitoplanktona nekega območja (Pakhomov E.A. in Froneman P.W., 2004; Bernard K.S., 2006; Elliot D.T. in sod., 2008). Pteropodi predstavljajo tudi pomemben plen za množico plenilcev višjih trofičnih nivojev, kot so mesojedi zooplankton, ribe, ptice in kiti (Lalli C.M. in Gilmer R.W., 1989; Hunt B.P.V. in sod., 2008).

Pteropodi igrajo pomembno vlogo v biogeokemijskih ciklih v oceanih, kot je na primer morska biološka črpalka ogljika, preko katere se organski in anorganski ogljik s površja prenašata v globine oceanov (Almogi-Labin A. in sod., 1988; Fabry V.J., 1989; Collier R. in sod., 2000). Organski ogljik pteropodi prispevajo v obliki teles mrtvih osebkov, metabolnih izločkov in z agregati, ki se tvorijo iz mukusnih mrež za lovljenje plena, skupaj z organskim materialom ujetim v njih (Bathmann U.V. in sod., 1991; Noji T.T. in sod., 1997; Accornero A. in sod.; 2003; Manno C. in sod., 2010). Transport anorganskega ogljika v s površja v globine poteka tako, da aragonitne lupine mrtvih pteropodov potonejo (Fabry V.J., 1989; Tsurumi M. in sod., 2005; Fabry V.J. in sod., 2008). V tropskih in subtropskih regijah z visoko nasičenostjo z aragonitom skozi celotni vodni stolpec, se na dnu oceana lahko zaradi kopičenja lupin pteropodov formirajo sedimenti, bogati z aragonitom (Lalli C.M. in Gilmer R.W., 1989; Almogi-Labin A. in sod., 1988; Honjo S. in sod. 2000, 2004; Hunt B.P.V. in sod., 2008; Bednaršek N. in sod., 2012a).

3 METODE

Raziskovalno delo je potekalo v obliki pregledovanja znanstvene literature in spletnih podatkovnih baz, z namenom zbrati vse obstoječe meritve gostote in biomase pteropodov iz redov Gymnosomata in Thecosomata ter hkrati zbirati podatke o fizičnih lastnostih pteropodov. Vir podatkov je bilo 36 strokovnih člankov in tri spletne

podatkovne baze. Zbranih je bilo 25 939 podatkovnih točk, izmed katerih je vsaka vsebovala informacijo o: času vzorčenja (leto, mesec, dan), lokaciji (zemljepisne koordinate), globini vzorčenja, klasifikaciji pteropodov, podatek o gostoti/biomasi, velikost uporabljene mreže in referenco. Po osnovnem pregledu in obdelavi podatkov je nastala baza 14 136 točk, v katero so bile vključene tudi meritve ničelne gostote pteropodov.

Večina zbranih podatkov so bile meritve gostote pteropodov, ki jih je bilo potrebno pretvoriti v biomaso. Pretvorbo sem izvedla na podlagi naslednjega razmerja:

Biomasa (mg m^{-3}) = Gostota (ind. m^{-3}) x Suha teža (mg m^{-3})

Suho težo sem izračunala na podlagi dolžine osebkov in njihove telesne geometrije. Podoben postopek so uporabili v projektu GLOBEC (Little W.S. in Copley N., 2003). Dolžine različnih vrst pteropodov sem določila na podlagi informacij pridobljenih na spletnem portalu za identifikacijo morskih vrst - Marine Species Identification Portal (http://species-identification.org/). Enačbe za pretvorbo so bile določene ali specifično za posamezno vrsto ali pa za posamezno skupino pteropodov s podobno telesno geometrijo, kadar enačba za določeno vrsto ni bila na voljo. Določila sem štiri kategorije pteropodov podobnih telesnih oblik: 1) ovalna, 2) trikotna/piramidna, 3) okrogla/globularna, 4) kornetasta/iglasta/stekleničasta.

Iz pridobljenih vrednosti biomase populacije pteropodov sem izračunala ogljikovo biomaso, s pomočjo konverzijskega faktorja 0,25 (Larson R.J.,1986) po principu:

Ogljikova biomasa (mg m^{-3}) = Suha teža (mg m^{-3}) x 0,25

Iz skupne biomase pteropodov s lupino sem izračunala karbonatni delež v skupni biomasi vseh pteropodov, s pomočjo spodnje enačbe:

$CaCO_3$ (%) = [Skupni ogljik (%) – Skupni organski ogljik (%)] x 8,33

Dr. Erik T. Buitenhuis (University of East Anglia) je podatkovno bazo z biomasami pteropodov pretvoril v NetCDF format, uporaben za delo v modeliranju (Buitenhuis E.T. in sod., 2012a).

Analiza podatkov je bila izvedena v programu Matlab v sodelovanju z mentorico Dr. Nino Bednaršek. Za izločanje visokih statističnih odstopanj je bil uporabljen Chauvenetov kriterij (Taylor R.J., 1996; Kirkup L., 2002; Buitenhuis E.T. in sod., 2012a).

4 REZULTATI

Rezultat raziskovalnega dela in zbiranja podatkov o gostoti/biomasi pteropodov sta dve podatkovni bazi – NetCDF format in baza s surovimi podatki (25 939). Bazi sta dostopni na spletnem portalu PANGEA (http://doi.pangaea.de/10.1594/PANGAEA.777384). Bazi vsebujeta naslednje podatke: lokacijo (koordinate) vzorčenja, globino in čas vzorčenja, meritev gostote pteropodov, ogljikovo biomaso pteropodov, podatke o velikosti mrežnih očesc na uporabljeni mreži. Baza s surovimi podatki vsebuje poleg tega še dodatne informacije o metodologiji vzorčenja in referenco. V Prilogi B je so zbrani podatki o fiziologiji pteropodov.

Analiziran podatkovni set je vseboval 15 134 podatkovnih točk, izmed katerih je bilo 10,6 % ničelnih vrednosti. Izmed vseh podatkov so 93% predstavljali pteropodi iz reda Thecosomata. Povprečna globalna biomasa pteropodov, brez ničelnih vrednosti, je znašala 4,58 mg C m^{-3} (std= 62,46), z mediano 0,0145 mg C m^{-3}. Na severni polobli je bila koncentracija biomase 4,04 mg C m^{-3} (std= 64,84), z mediano 0,02 mg C m^{-3} in na južni polobli 8,15 mg C m^{-3} (std= 45,35), z mediano 0,001 mg C m^{-3}. Maksimalni koncentraciji biomase pteropodov iz obeh redov Thecosomata in Gymnosomata sta bili zabeleženi na severni polobli in sta znašali 2979,7 mg C m^{-3} in 5045 mg C m^{-3}.

Povprečna biomasa pteropodov s lupinami je znašala 3,81 mg C m^{-3} (std= 40,24), kar predstavlja 83 % globalne biomase vseh pteropodov. Povprečna karbonatna biomasa pteropodov z lupinami je znašala 8,57 mg $CaCO_3$ m^{-3}.

Izračun letne produkcije ogljika pteropodov je znašal 444–505 Tg C $leto^{-1}$. Pteropodi s lupinami letno proizvedejo 828,838-942,714 Tg CaCO3 $leto^{-1}$. Ta vrednost je primerljiva z izračuni v študiji Gangstø R. in sod. (2008), kjer letna proizvodnja karbonata, ki ga v večini prispevajo pteropodi, znaša 0,3 Pg C $leto^{-1}$.

Podatki meritev biomase, vključeni v bazo so bili zbrani v času med 1950–2010. Najmanj meritev je bilo izvedenih v 80-ih letih in okoli leta 2010, največ med 1960–1970. Relativno konsistentno je pokrito tudi obdobje med 1990–2000. Na severni polobli se je vzorčenje sistematično izvajalo skozi vse letne čase. Na južni polobli je bilo več vzorčenja izvedenega pozimi in poleti, kot pa v ostalih dveh letnih časih.

Ne-ničelne meritve biomase pteropodov so bile izvedene v vseh 10° pasovih zemljepisne širine. Kar 77% meritev je bilo izvedenih na severni polobli, največ med 30°- 40°. Visoke koncentracije biomase so bile izmerjene na raznolikih zemljepisnih širinah. Na severni polobli je bila najvišje povprečna biomasa izmerjene v srednjih zemljepisnih širinah in je padala proti ekvatorju in severnemu polu. Na južni polobli je bil viden trend padanja biomase od pola proti ekvatorju.

Pteropodi so se pojavljali med površjem in globino 2000 m. V zgornjih 200 m je bilo izvedenih 83% meritev, kjer je bilo zabeleženo tudi 62% celotne biomase pteropodov. Preostalih 38% biomase je bilo enakomerno razporejene do 1000 m globine, z redkimi pozitivnimi meritvami pod 1000 m. Najvišje biomase so bile izmerjene blizu površja (0-10 m), s povprečno biomaso 20,65 mg C m^{-3} (std= 157,81), mediano 0,02 mg C m^{-3} in maksimalno biomaso 5045 mg C m^{-3}.

Na severni polobli je bila najvišja povprečna biomasa pteropodov (5,42 mg C m^{-3}) izmerjena spomladi, maksimalna (5,05e+003 mg C m^{-3}) pa poleti. Na južni polobli je bila najvišja povprečna biomasa (39,71 mg C m^{-3}) izmerjena spomladi, maksimalna (608,35 mg C m^{-3}) pa prav tako spomladi. Na južni polobli je bilo opaziti večja nihanja oz. razlike med povprečnimi biomasami v različnih letnih časih.

V procesu obdelave in analize podatkov so se pojavile določene napake. Večkrat v viru podatkov ni bilo specificirano ali so izmerjene gostote pteropodov meritve odraslih ali mladih osebkov. V teh primerih bi lahko v procesu preračunavanja gostote v biomaso prišlo do precenitve oz. podcenitve koncentracije biomase.

Pri vzorčenju pteropodov so bile uporabljene različne tehnike, npr. mreže z različnimi velikostmi mrežnih očes (100-3000 µm). To bi lahko vplivalo na rezultate meritev gostote/biomase pteropodov in s tem na rezultate analize podatkov v tej raziskovalni nalogi. V 19 671 primerih meritev je bil dostopen podatek o velikosti mrežnih očes

uporabljenih mrež. Slednje je omogočilo izvedbo analize, ki je pokazala, da velikost mrežnih očes v primeru te študije nima bistvenega vpliva na rezultate. Tako ni bilo potrebno na podlagi tega izločiti nobene meritve. Prav tako se je izkazalo, da ni bila nobena specifična velikost mrežnih očesc uporabljena bolj pogosto na specifični zemljepisni širini/dolžini. V nasprotnem primeru bi to lahko vplivalo na prikaz globalne razširjenosti biomase pteropodov. Vendar pa napaka zaradi primerjave tako velikega obsega podatkov pridobljenih z različnimi merilnimi/vzorčevalnimi tehnikami vseeno obstaja. V podatkovni bazi so zato ob vsaki meritvi, kjer so bile le te dostopne, pripisane dodatne informacije o tehnikah vzorčenja.

Navsezadnje je možno potrditev, da so preračunane biomase vendarle v pravem velikostnem razredu, izpeljati na podlagi primerjave le teh z originalnimi biomasami. 11% zbranih podatkov v podatkovni bazi so bili namreč originalne biomase, podane že v virih podatkov. Ostalih 89% so bile meritve gostote pteropodov, ki so bile za potrebe analize te študije pretvorjene v biomaso. V primerjavi z najvišjo originalno biomaso (538 mg C m^{-3}) tekosomatov, je bila najvišja preračunana biomasa (2979,7 mg C m^{-3}) tekosomatov le za en velikostni razred večja. Taki rezultati primerjave potrjujejo ustreznost izbrane metodologije za obdelavo podatkov.

5 DISKUSIJA

Skozi diskusijo je narejen pregled možnosti vpliva okoljskih dejavnikov, ki so posledica klimatskih sprememb, na pteropode. Okoljski dejavniki vzeti pod drobnogled so zakisljevanje, deoksigenacija in segrevanje oceanov. Podlaga za napovedovanje trendov v odzivu pteropodov na spremembe v njihovem življenjskem okolju, so rezultati analize globalne porazdelitve oz. razširjenosti biomase pteropodov in njihove fizične značilnosti ter omejitve, opisane v teoretičnem delu.

5.1 Segrevanje

Segrevanje oceanov je posledica zviševanja koncentracije ogljikovega dioksida v ozračju in okrepljenega efekta tople grede (IPCC, 2007). Oceani sprejmejo velik del toplote, ujete v zemeljski atmosferi, zaradi česar se je v zadnjih 100 letih površina oceanov segrela za 0,7 °C (IPCC, 2007). Segrevanje oceanov ni enotno na globalni ravni, saj je na primer odvisno od koncentracije aerosolov nad posameznim delom zemeljskega površja (Bartnett T.P in sod., 2005). Največji dvig temperature je pričakovati v tropih in na območju visokih zemljepisnih širin na severni polobli (Gruber N., 2011). Posledica segrevanja oceanov je taljenje morskega ledu (Yin J. in sod., 2001), sprememba v slanosti (IPCC, 2007), povečana stratifikacija zgornjih plasti in posledično spremenjen transport hranil ter kisika v vodnem stolpcu (Gruber N., 2011). Pričakovati je spremembe v primarni produkciji – v vrstni sestavi fitoplanktona, v času pojava povečane primarne produkcije in upad/rast primarne produkcije v specifičnih regijah (Behrenfeld M.J. in sod., 2006).

Na morske živali bo direktno vplivalo segrevanje življenjskega okolja, saj bodo spremembe temperature presegle obseg njihovih temperaturnih niš, zaradi česar se bo potencialno zmanjšala stabilnost populacij (Pörtner H.-O. 2008, 2010). Morske živali, ki se ne bodo zmožne prilagoditi na spremenjene razmere v njihovem primarnem okolju, bodo spremenile svojo razširjenost (Pörtner H.-O. 2008, 2010). Takšne spremembe v razširjenosti pteropodov, npr. selitve v hladnejša območja, bi bilo pričakovati tudi s strani pteropodov (Comeau S. in sod., 2011). Indirektno bodo posledice segrevanja na pteropode lahko vplivale preko sprememb v primarni produkciji. Njihova gostota in

dnevna ter sezonska razširjenost, skozi analize zabeleženi kot najvišji na površju in sezonsko pomladi ter poleti, potrjujeta povezavo z (visoko) primarno produkcijo. Zmanjšanje produktivnosti fitoplanktona je predvideno predvsem v srednjih in nizkih zemljepisnih širinah (Behrenfeld M.J. in sod., 2006; Martinez E. in sod., 2009), povečanje produkcije pa na območjih visokih zemljepisnih širin (Richardson A.J. in Shoeman D.S., 2004; Steinacher M. in sod., 2009). To bi lahko dodatno stimuliralo selitve pteropodov v hladnejša območja. Spremembe v vrstni sestavi fitoplanktona, ki bo predvidoma v prihodnosti težila k manjšim vrstam (Moran X.A.G. in sod., 2010), bi lahko pozitivno vplivale na določene vrste pteropodov, za katere je to preferenčna velikost hrane (Perissinotto R., 1992; Bernard K.S., 2006). Po drugi strani bi lahko spremembe v času pojava povišane primarne produkcije ali pa povečane energijske potrebe pteropodov zaradi višjih temperatur v času pomanjkanja hrane (Seibel B.A. in sod., 2007; Comeau S. in sod., 2010), negativno vplivale na stabilnost populacije pteropodov (Seibel B.A. and Dierssen H.M., 2003; Bernard K.S. in Froneman P.W., 2009).

5.2 Deoksigenacija

Zaradi segrevanja oceanov se manj kisika raztaplja v vodi, posledica stratifikacije zgornjega dela vodnega stolpca pa je tudi slabša cirkulacija s kisikom bogatejše vode s površja v notranjost oceanov (Keeling R.F. in sod., 2010). Zaradi povečane stratifikacije na nekaterih območjih, naj bi se zvišala stopnja primarne produkcije na površju, kar bi zaradi večjega dovajanja organskih snovi v nižje vodne plasti povzročilo nesorazmernost porabe in dovoda kisika v teh plasteh (Keeling R.F. in sod., 2010). Globalna koncentracija kisika v oceanih naj bi v naslednjih sto letih upadla za 1-7 %, razširile naj bi se cone z minimalno koncentracijo kisika, ki se trenutno najpogosteje pojavljajo okoli termokline (med 400-1200 m), vse to pa bo povišalo možnost izpostavljenosti morskih živali stresu zaradi hipoksije (Karstensen J. in sod., 2008; Keeling R.F. in sod., 2010; Seibel B.A., 2011). Koncentracija kisika pri kateri pteropodi doživijo hipoksijo in sposobnost preživetja v hipoksičnem okolju se močno razlikujeta med vrstami, zato so vrste različno ranljive za vpliv deoksigenacije oceanov (Seibel B.A., 2011; Maas A.E. in sod., 2012b).

V vzhodnem tropskem Pacifiku živijo vrste pteropodov, ki migrirajo v cone z minimalno koncentracijo kisika in so sposobne določen čas preživeti v hipoksičnem okolju (Maas A.E. in sod., 2012b). To je bilo razvidno tudi iz analize razširjenosti biomase pteropodov – pozitivne meritve biomase so bile zabeležene v znanih območjih z nizko koncentracijo kisika. Podoben trend v razširjenosti je bilo opaziti v Indijskem Oceanu. Pteropodi omenjenih dveh tropskih območjih bi lahko bili, zaradi obstoječih prilagoditev na hipoksijo, manj ranljivi za posledice deoksigenacije oceanov. Poleg tega naj bi v koncentraciji kisika v vodi v tropih prišlo le do manjših sprememb (Keeling R.F. in sod., 2010), kar dodatno zmanjša možnosti izpostavljenosti bolj ekstremni hipoksiji za pteropode v Indijskem Oceanu in tropskem Pacifiku. Bolj ranljivi bi po drugi strani lahko bili pteropodi živeči v Severnem Pacifiku, kjer se razširjenost biomase pteropodov iz rezultatov analize ne prekriva z območji nizkih koncentracij kisika. Slednje bi lahko pomenilo, da so pteropodi iz tega območja neprilagojeni na uspešno preživetje v hipoksičnem okolju, ki naj bi se v prihodnosti v subarktičnem Severnem Pacifiku razširilo na globino 200-400 m (Plattner G.K. in sod., 2001). Pričakovani odzivi živali na hipoksijo so spremembe v razširjenosti, uspešnosti in vitalnosti populacij ter ogrožanje preživetja živali določenih območij (Seibel B.A. in Dierssen H.M., 2009).

5.3 Zakisljevanje

Koncentracija CO_2, v zemeljskem ozračju se zvišuje zaradi deforestacije, kurjenja fosilnih goriv, izpustov cementne industrije ter zaradi drugih človekovih dejavnosti (Sabine C.L. in sod., 2004). Velik delež CO_2 iz ozračja absorbirajo oceani, posledica česar je nižanje pH in zviševanje parcialnega tlaka CO_2 (pCO_2) ali tako imenovano zakisljevanje oceanov (Sabine C.L. in sod., 2004; Raven J. in sod., 2005). Zaradi zakisljevanja, lokalno povečane količine padavin in taljenja morskega ledu, naj bi upadla koncentracija karbonatnih ionov v oceanih, zaradi česar se bodo začela širiti območja nenasičenosti z aragonitom (Orr C.J. in sod., 2005; Steinacher M. in sod., 2009; Gruber N., 2011). To bo še posebno prizadelo morske organizme, kot so pteropodi, ki v z aragonitom nenasičenih območjih manj učinkovito tvorijo svoje aragonitne lupine, ki so ob enem podvržene tudi raztapljanju (Or C.J. in sod., 2005; Comeau S. in sod. 2009, 2010a, 2010b; Lischka S. in sod., 2011; Bednaršek N. in sod., 2012b).

Odzivi pteropodov na zakisljevanje in posledično na za njihove aragonitne lupine korozivne razmere v okolju, so potencialno lahko evolucijske prilagoditve, kot sta pospešena rast/kalcifikacija ali spremembe v mineralni sestavi lupine (Bednaršek N., 2010; Lischka S. in sod., 2011). Možne so tudi spremembe v goegrafski in vertikalni razširjenosti pteropodov (Hunt B.P.V. in sod., 2008; McNeil B.I. in Matear R.J., 2008; Comeau S. in sod., 2011; Seibel B.A., 2011; Bednaršek N. in sod., 2012b) ter v najslabšem primeru izginotje pteropodov iz najbolj prizadetih regij oceanov (Comeau S. in sod., 2011; Bednaršek N. in sod., 2012b). Slednje so primarno polarna območja, ki naj bi po napovedih dosegla lokalno nenasičenost z aragonitom v vrhnjih plasteh vodnega stolpca že v naslednjih desetletjih, skozi celotni vodni stolpec pa do konca tega stoletja (Orr C.J. in sod., 2005; McNeil B.I. in Matear R.J., 2008; Steinacher M. in sod., 2009). Iz podatkov o globalni razširjenosti pteropodov je razvidno, da so pteropodi že v tem trenutku po vsej verjetnosti na določenih območjih v polarnih regijah izpostavljeni nizki nasičenosti oz. nenasičenosti z aragonitom. To trditev potrjujejo rezultati opazovane študije Bednaršek N. in sod. (2012b), izvedene na pteropodih v določeni regiji Južnega Oceana. Analiza razporeditve globalne biomase pteropodov je potrdila tudi, da populacije pteropodov lahko dosežejo najvišje gostote prav v območjih visokih zemljepisnih dolžin, kjer torej predstavljajo pomemben del ekosistemov. Vsakršne spremembe v razširjenosti ali številčnosti pteropodov v teh regijah zaradi zakisljevanja, bi potemtakem lahko imele občutne posledice za celotne ekosisteme.

7 ZAKLJUČEK

Pteropodi so pomemben del v prehranjevalnih verigah morskih ekosistemov ter igrajo vlogo v biogeokemijskih ciklih v oceanih, zato je pomembno, da jih kot eno izmed relevantnih planktonskih funkcionalnih skupin vključujemo v biogeokemijske modele in modele morskih ekosistemov (Hood R.R. in sod., 2006; Le Quéré C. in sod., 2009). Podatki o globalni razširjenosti biomase pteropodov in fizičnih lastnostih pteropodov, zbrani skozi raziskovalno delo tega diplomskega dela, so pomembni za izgradnjo in preverjanje takšnih modelov. Analiza nabora podatkov biomase pteropodov je bila objavljena v strokovnem članku v posebni izdaji znanstvene revije ESSD (glej Bednaršek N. in sod., 2012c), kot ena izmed desetih podobnih analiz pomembnih planktonskih funkcionalnih skupin projekta MAREDAT. Za nabor podatkov, ki vsebuje informacije o fizičnih lastnostih pteropodov, je načrtovana uporaba v modeliranju v sodelovanju s strokovnjaki iz UEA (University of East Anglia) v bližnji prihodnosti.

Na podlagi pregleda možnih vplivov zakisljevanja, deoksigenacije in segrevanja morja na pteropode lahko zaključim, da so pteropodi dovzetni za vplive vseh treh okoljskih dejavnikov, ki lahko na pteropode vplivajo tudi v sinergiji eden z drugim. Napovedovanje odzivov pteropodov na globalne spremembe v oceanih je kompleksno, prav zaradi možne sinergije med delujočimi okoljskimi dejavniki in zaradi raznolikosti odzivov med različnimi vrstami in življenjskimi stadiji pteropodov na te stresne dejavnike. Splošne posledice vplivov zakisljevanja, deoksigenacije in segrevanja oceanov bodo najverjetneje spremembe v gostoti in razširjenosti pteropodov. Vplivi bodo zgodnji in močni posebno v polarnih ekosistemih, iz katerih bi pteropodi lahko v prihodnosti tudi popolnoma izginili. Izguba pteropodov iz morskih ekosistemov ima negativen vpliv na ravnovesje v prehranjevalnih verigah, kot tudi potencial za zmanjšanje učinkovitosti biološke črpalke ogljika v oceanih. Analiza produkcije ogljika in karbonata pteropodov je namreč pokazala, da tekosomati prispevajo pomemben delež k globalni produkciji karbonata.

8 REFERENCE

Accornero A., Manno C., Esposito F., Gambi, M. C. 2003. The vertical flux of particulate matter in the polyna of Terra Nova Bay. Part II. Biological components. *Antarctic Science*, 15, 175-188

Almogi-Labin A., Hemleben C., Deuser W.G. 1988. Seasonal variation in the flux of euthecosomatous pteropods collected in a deep sediment trap in Sargasso Sea. *Deep-Sea Research*, 35, 3: 441-464

Ashjian C.J., Cabell S.D., Gallager S.M., Alatalo P. Distribution of plankton, particles, and hydrographic features across Georges Bank described using the Video Plankton Recorder. Dee-Sea research Part II, 48, 245-282

Barnett T.P, Pierce D.W., AchutaRao K.M., Glecker P.J., Santer B.D., Gregory J.M., Washington W.M. 2005. Penetration of Human-Induced Warming into World's Oceans. *Science,* 309, 284-287

Bathmann U.V., Noji T.T., von Bodungen B. 1991. Sedimentation of pteropods in the Norwegian Sea in autumn. *Deep-Sea Research*, 38, 10: 1341-1360

Bednaršek, N. 2010. Vulnerability of Southern Ocean pteropods to anthropogenic ocean acidification. PhD. University of East Anglia. School of Environmental Sciences

Bednaršek N., Tarling G.A., Bakker D.C.E. 2012a. Population dynamics and biogeochemical significance of *Limacina helicina antarctica* in the Scotia Sea (Southern Ocean). *Deep-Sea Research II: Tropical Studies in Oceanography*, 59-60, 105-116

Bednaršek N., Tarling G.A., Bakker D.C.E., Fielding S., Jones E.M., Venables H.J., Ward P., Kuzirian A., Lézé B., Feely R.A., Murphy E.J. 2012b. Extensive dissolution of live pteropods in the Southern Ocean. *Nature Geoscience*, 5, 881-885, doi: 10.1038/ngeo1635

Bednaršek N., Možina J., Vogt M., O'Brien C., Tarling G.A. 2012c. The global distribution of pteropods and their contribution to carbonate and carbon biomass in the modern ocean. *Earth System Science Data,* 4, 167-186

Behrenfeld M.J., O'Malley R.T., Siegel D.A., McClain C.R., Sarmiento J.L., Feldman G.C., Milligan A.J., Falkowski P.G., Letelier R.M., Boss E.S. 2006. Climate-driven trends in contemporary ocean productivity. *Nature, Letters*, 444, doi: 10.1038/nature05317

Bernard K. S. 2006. The role of the euthecosome pteropod *Limacina retroversa*, in the Polar Frontal Zone, Southern Ocean. PhD. Rhodes University.

Bernard K.S., Froneman P.W. 2009. The sub-Antarctic euthecosome pteropod, *Limacina retroversa*: Distribution patterns and trophic role. *Deep-Sea Research I*, 56, 582-598

Bryan P.J., Yoshida W.Y., McClintock J.B., Baker B.J. 1995. Ecological role for pteroenone, a novel antifeedant from the conspicuous antarctic pteropod *Clione antarctica* (Gymnosomata: Gastropoda). *Marine Biology*, 122, 2: 271-277

Böer M., Gannefors C., Kattner G., Graeve M., Hop H., Falk-Petersen S. 2005. The Arctic pteropod *Clione limacina*: seasonal lipid dynamics and life-strategy. *Marine Biology*, 147:707-717

Böer M., Kattner G., Graeve M. 2006. Impact of feeding and starvation on the lipid metabolism of the Arctic pteropod *Clione limacina. Journal of Experimental Marine Biology and Ecology,* 328, 98-112

Böer M., Graeve M., Kattner G. 2007. Exceptional long-term starvation ability and sites of lipid storage of the Arctic pteropod *Clione limacina*. *Polar Biology*, 30, 571-580

Buitenhuis E. T., Vogt, M., Bednaršek N., Doney S.C., Leblanc C., Quéré C.L., Luo Y.-W. , Moriarty M., O'Brien C., O'Brien T., Peloquin J., Schiebel R. 2012a (under review). MAREDAT : Towards a World Ocean Atlas of MARine Ecosystem DATa. *Earth Systems Science Data (Open Access Discussions)*, 5, 1077-1106, doi:10.5194/essdd-5-1077-2012

Byrne M. 2011. Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. *Oceanography and Marine Biology: An annual review*, 49, 1-42

Christou E.D., Moraitou-Apostolopoulou M. 1995. Metabolism and feeding of mesozooplankton in the eastern Mediterranean (Hellenic coastal waters). *Marine Ecology Progress Series*, 126, 39-48

Collier R., Dymond J., Honjo S., Manganini S., Francois R. 2000. The vertical flux of biogenic and lithogenic material in the Ross Sea: moored sediment trap observations 1996–1998. *Deep-Sea Research Part II,* 47, 3491–3520

Comeau S., Gorsky G., Jeffree R., Teyssié J.-L., Gattuso J.-P. 2009. Impact of ocean acidification on a key Arctic pelagic mollusc (*Limacina helicina*). *Biogeosciences*, 6, 1877–1882

Comeau S., Jefferee R., Teyssie J.-L., Gattuso J.-P. 2010a. Response of the Arctic Pteropod *Limacina helicina* to Projected Future Environmental Conditions. *PLoS ONE*, 5 (6)

Comeau S., Gorsky G., Alliouane S., Gattuso J. P. 2010b. Larvae of the pteropod *Cavolinia inflexa* exposed to aragonite undersaturation are viable but shell-less. *Marine Biology*, 157, 2341–2345

Comeau S., Gattuso J.-P., Nisumaa A.-M., Orr J. 2011. Impact of aragonite saturation state changes on migratory pteropods. *Proceedings of The Royal Scociety of London, Series B.: Biological Sciences,* 279, 732-738, doi: 10.1098/rspb.2011.0910

Dadon J.R., de Cidre L.L. 1992. The reproductive cycle of the Thecosomatous pteropod *Limacina retroversa* in the western South Atlantic. *Marine Biology*, 114, 439-422

Doney S.C., Fabry V.J., Feely R.A., Kleypas J.A. 2009. Ocean acidification: the other CO_2 problem. *Annual Review of Marine Science*, 1, 169-192

Elliot D.T., Tang K.W., Shields A.R. 2008. Mesozooplankton beneath the summer sea ice in McMurdo Sound, Antarctica: abundance, species composition, and DMSP content. *Polar Biology*, 32, 113-122

Fabry, V. J. 1989. Aragonite production by pteropod molluscs in the subarctic Pacific, Deep Sea Research Part A. *Oceanographic Research Papers*, 36, 11: 1735-1751

Fabry V.J., Seibel B.A., Feely R.A., Orr C.J. 2008. Impacts of ocean acidification on marine fauna and ecosystem process. *ICES Journal of Marine Science*, 65, 414-432

Falk-Petersen S., Leu E., Berge J., Kwasniewski S., Nygård H., Røstad A., Keskinen E., Thormar J., von Quillfeldt C., Wold A., Gulliksen B. 2008. Vertical migration in high Arctic waters during autumn 2004. *Deep-Sea Research II*, 55, 2275-2284

Feely R. A., Sabine C. L., Kitack L., Berelson W., Kleypas J., Fabry V. J., Millero F. J. 2004. Impact of Anthropogenic CO_2 on the $CaCO_3$ System in the Oceans. *Science*, 305, 5682: 362–366, doi: 10.1126/science.1097329

Gangstø R., Gehlen M., Schneider B., Bopp L., Aumont O., Joos F. Modeling the marine aragonite cycle: changes under rising carbon dioxide and its role in shallow water CaCO3 dissolution. *Biogeosciences*, 5, 1057-1072

Gannefors C., Böer M., Kattner G., Graeve M., Eiane K., Gulliksen B., Hop H., Falk-Petersen S. 2005. The Arctic sea butterfly *Limacina helicina*: lipids and life strategy. *Marine Biology*, 147: 169-177

Gilmer R.W. 1972. Free-floating mucus webs: a novel feeding adaptation for the open ocean. *Science*, 176, 1239-1240

Gilmer R.W., Harbison G.R. 1991. Diet of *Limacina helicina* (Gastropoda:Thecosomata) in Arctic waters in midsummer. *Marine Ecology Progress Series*, 77 , 125-134

Gilmer, R.W. 1990. In situ observations of feeding in thecosomatous pteropod molluscs, *American Malacological Bulletin*, 8, 1: 53-59

Gilmer R.W., Harbison G.R. 1986. Morphology and field behaviour of pteropod molluscs: feeding methods in the families Cavoliniidae, Limacinidae and Peraclididae (Gastropoda: Thecosomata), *Marine Biology*, 91, 47-57

Gruber N. 2011. Warming up, turning sour, losing breath: ocean biogeochemistry under global change. *Philosophical Transactions of the Royal Society A, Mathematical, physical & Engeneering Sciences*, 369, 1980-1996

Hofmann G.E., Todgham A.E. 2010. Living in the Now: Physiological Mechanisms to Tolerate a Rapidly Changing Environment. *Annual Review of Physiology*, 72, 127-45, doi: 10.1146/annurev-physiol-021909-135900

Honjo S. 2004. Particle export and the biological pump in the Southern Ocean. *Antarctic Science*, 16, 501–516.

Honjo S., Francois R., Manganini S., Dymond J., Collier R. 2000. Particle fluxes to the interior of the Southern Ocean in the Western Pacific sector along 170° W. *Deep Sea Research Part II,* 47, 3521–3548

Hood R.R., Laws E.A., Armstrong R.A., Bates N.R., Brown C.W., Carlson C.A., Chai F., Doney S.C., Falkowski P.G., Feely R.A., Friedrichs M.A.M., Landry M.R., Moore J.K., Nelson D.M., Richarson T.L., Saluhoglu B., Schartau M., Toole D.A., Wiggert J.D. 2006. Pelagic functional group modelling: Progress, Challenges and prospects. *Deep-Sea Research II*, 53, 459-512

Hunt B.P.V., Pakhomov E.A., Hosie G.W., Siegel V., Ward P., Bernard K. 2008. Pteropods in Southern Ocean ecosystems, *Progress in Oceanography.* 78, 3: 193-221

IPCC - Climate change 2007: Working Group I: The physical science basis. IPCC Fourth Assessment Report: Climate Change 2007of the Intergovernmental Panel on Climate Change (Eds. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor & H. Miller). Cambridge, UK: Cambridge University Press

Karstensen J., Stramma L., Visbeck M. 2008. Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. *Progress in Oceanography,* 77, 331-350

Keeling R. F., Körtzinger A., Gruber N., N. 2010. Ocean deoxygenation in a warming world. *Annual Review of Marine Science*, 2, 199-229

Kirkup L. 2002. Data Analysis with Excel®: An Introduction for Physical Scientists. Cambridge University Press, 1st edition (March 18, 2002), pp. 184-186

Kobayashi, H.A. 1974. Growth cycle and related vertical distribution of the thecosomatous pteropod *Spiratella* (‘‘*Limacina*’’) *helicina* in the central Arctic Ocean. *Marine Biology*, 26, 295-301

Lalli C.M., Gilmer R.W. 1989. Pelagic snails: The Biology of Holoplanktonic Gastropod Molluscs. Stanford, Stanford University Press

Le Quéré C., Harrison S.P., Prentice C., Buitenhuis E.T, Aumonts O., Bopp L., Claustre H., da Cunha L.C., Geider R., Giraud X., Klaas C., Kohfeld K.E., Legendre L., Manizza M., Plattss T., Rivkin R., Sathyendranath S., Uitz J., Watson A.J., Wolf-Gladrow, D. 2005 Ecosystem dynamics based on plankton functional types for global ocean biochemistry models. *Global Change Biology,* 11, 2016-2040

Le Quéré C., Sathyendranath S., Meike V., Buitenhuis E.T., Bopp L., Doney S., Dutkiewicz S., Geider R.J., Harrison S., Klaas C., Legendre L., Pesant S., Platt T., Prentice C., Rivkin R., Wolf-Gladrow D., Yamanaka Y. 2009. Observational needs of Dynamic Green Ocean Models, Proceedings of OceanObs'09: Sustained Ocean Observations and Information for Society (Vol. 2). Venice Italy, 21-25 September 2009, Hall J., Harrison D.E. & Stammer D., Eds., ESA Publication WPP-306, doi: 10.5270/OceanObs09.cwp.56

Lischka S., Büdenbender J., Boxhammer T., Riebesell U. 2011. Impact of ocean acidification and elevated temperatures on early juveniles of the polar shelled pteropod *Limacina helicina*: mortality, shell degradation, and shell growth. *Biogeosciences*, 8, 919-932

Little W.S., Copley N.J. 2003. WHOI Silhouette DIGITIZER, Version 1.0, Users Guide, WHOI Technical Report, Woods Hole Oceanographic Institution

Maas A.E., Elder L.E., Dierssen H.M., Seibel B.A. 2011. Metabolic response of Antarctic pteropods (Mollusca: Gastropoda) to food deprivation and regional productivity. *Marine Ecology Progress Series*, 441, 129-139

Maas A.E., Wishner K.F., Seibel B.A. 2012a. The metabolic response of pteropods to acidification reflects natural CO_2-exposure in oxygen minimum zones. *Biogeosciences*, 9, 747-757

Maas A.E., Wishner K.F., Seibel B.A. 2012b. Metabolic suppresion in the thecosomeatous pteropods as an effect of low temperature and hypoxia in the eastern tropical North Pacific, *Marine Biology*, 159, 1955-1967

Mackas D.L. and Galbraith M.D. 2002. Zooplankton Distribution and Dymnamics in North Pacific Eddy of Coastal Origin: I. Transport and Loss of Continental Margin Species. *Journal of Oceanography*, 58, 725-738

Manno C., Tirelli V., Accornero A., Fonda Umani S. 2010. Importance of the *Limacina helicina* faecal pellets contribution to the carbon pump, (Terra Nova Bay, Antarctica). *Journal of Plankton Research*, 32, 2: 145-152

Martinez E., Antoine D., D'Ortenzio F., Gentili B. 2009. Climate-Driven Basin-scale Decadal Oscillation of Oceanic Phytoplankton. *Science,* 326, 1253, doi: 10.1126/science.1177012

McNeil B.I., Matear R.J. 2008. Southern Ocean acidification: A tipping point at 450-ppm, atmospheric CO_2. *PNAS,* 105, 48: 18860-18864

Mileikovsky S.A. 1970. Breeding and larval distribution of the pteropod *Clione limacina* in the North Atlantic, Subarctic and North Pacific Oceans. *Marine Biology*, 6, 317-332

Morán X.A.G., Lopez-Urrutia A., Calvo- Díazi A., Li W.K.W. 2010. Increasing Importance of small phytoplankton in warmer ocean. Global Change Biology, 16, 3: 1137-1144, 10.1111/j.1365-2486.2009.01960.x

Noji T.T., Bathmann U.V., von Bodungen B., Voss M., Antia A., Krumbholz M., Klein B., Peeken I., Noji C.I.-M., Rey F. 1997. Clearance of picoplankton-sized particles and formation of rapidly sinking aggregates by the pteropods, *Limacina retroversa. Journal of Plankton Research,* 19, 7: 863-875

Orr C.J., Fabry V.J., Aumont O., Bopp. L., Doney S.C., Feely R.A., Gnanadesikan A., Gruber N., Ishida A., Joos F., Key R.M., Lindsay K., Maier-Reimer E., Matear R., Monfray P., Mouchet A., Najjar R.G., Plattner G.-K., Rodgers K.B., Sabine C.L., Sarmiento J.L., Schlitzer, R., Slater R.D., Totterdell I.J., Weirig M.-F., Yamanaka Y., Yool A. 2005. Anthropogenic ocean acidification over twenty-first century and its impact on calcifying organisms. *Nature,* 437

Pakhomov E.A., Froneman P.W. 2004. Zooplankton dynamics in the eastern Atlantic sector of the Southern Ocean during the austral summer 1997/1998-Part 2: Grazing impact. *Deep-Sea Research II*, 51, 2617-2631

Pane L., Feletti, M., Francomacaro B., Mariottini G.L. 2004. Summer coastal zooplankton biomass and copepod community structure near Italian Terra Nova Base (Terra Nova Bay, Ross Sea, Antarctica). *Journal of Plankton Research*, 26, 12: 1479-1488

Perissinotto R., McQuaid C.D. 1992. Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean archipelago. *Marine Ecology Progress Series,* 80, 15-27

Pinsonneault A.J., Matthews H.D., Galbraith E.D., Schmittner A. 2012. Calcium carbonate production response to the future ocean warming and acidification. *Biogeosciences*, 9, 2351-2364, doi: 10.5194/bg-9-2351-2012

Plattner G.K., Joos F., Stocker T.F., Marchal O. 2001. Feedback mechanisms and sensitivities of ocean carbon uptake under global warming. *Tellus Series B-Chemical and Physical Meteorology,* 53, 5, 564–92, doi: 10.1034/j.1600-0889.2001.530504.x

Pörtner H.-O. 2001. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. Naturwissenschaften, 88, 137-146, doi: 10.1007/s001140100216

Pörtner H.-O. 2002. Review. Physiological basis of temperature-dependent biogeography: trade-offs in muscle design and performance in polar ectotherms. *The Journal of Experimental Biology*, 205, 2217-2230

Pörtner H.-O. 2008. Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. *Marine Ecology Progress Series,* 373, 203-217, doi: 10.3354/meps07768

Pörtner, H.-O. 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology,* 213, 881–893, doi:10.1242/jeb.0375523

Raven J., Caldeira K., Elderfield H., Hoegh-Guldberg O., Liss P., Riebesell U., Shepherd J. Turley C., Watson A. 2005. Ocean acidification due to increasing atmospheric carbon dioxide.*The Royal Society*, a policy document, London, UK

Redfield A.C. 1939. The history of population of *Limacina retroversa* during its drift across the Gulf of Maine. *Biological Bulletin*, 76 (1)

Richardson A.J., Schoeman D.S. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, 305, 1609-16012

Rosenthal J.J.C, Seibel B.A., Dymowska A., Bezanilla. 2012. Trade-off between aerobic capacity and locomotors capability in an Antarctic pteropod. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 15: 6192-6196

Schalk, P. H. 1990. Spatial and seasonal variation in pteropods (Mollusca) of Indo-Malayan waters related to watermass distribution. *Marine Biology*, 105, 59-71

Sabine C. L., Feely R. A., Gruber N., Key R. M., Lee K., Bullister J. L., Wanninkhof R., Wong C. S., Wallace D. W. R.., Tilbrook B, Millero F. J., Peng T. H., Kozyr A., Ono T., Rios A. F. 2004. The oceanic sink for anthropogenic CO_2. *Science,* 305, 367–371, doi:10.1126/science.1097403

Sabine C.L., Feely R.A. 2007. The Oceanic Sink for Carbon Dioxide. Greenhouse Gas Sinks, Reay D., Hewitt N., Grace J., Smith K. (Eds.), CABI, Oxfordshire, UK

Seibel B.A. 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *The Journal of Experimental Biology*, 214, 326-336

Seibel B.A., Dierssen H.M. 2003. Cascading trophic impacts of reduced biomass in the Ross Sea Antarctica: just the tip of the iceberg?. *Biological Bulletin,* 205, 93–97

Seibel B.A., Dierssen H. M. 2009. Perspective: animal function at the heart (and gut) of oceanography. *Science*, 323, 343-344

Seibel B.A., Dymowska A., Rosenthal J. 2007. Metabolic temperature compensation and coevolution of locomotory performance in pteropod molluscs. *Integrative and Comparative Biology*, 47, 6: 880-891

Seibel B.A., Maas A.E., Dierssen H.M. 2012. Energetic Plasticity Underlies a Variable Response to Ocean Acidification in the Pteropod, *Limacina helicina antarctica*. *PLoS ONE* 7, 4: e30464

Silverman J., Lazar B., Erez J. 2007. Effect of aragonite saturation, temperature and nutrients on the community calcification rate of coral reef. *Journal of Geophysical Research*, 112, C05004, doi:10.1029/2006JC003770

Skelet B., Gogala M., Kuštor V. (Eds.). 2003. Živalstvo Slovenije., 1. natis. Ljubljana, Tehniška Založba Slovenije: str. 119

Smith K.L. Jr., Teal J.M. 1973. Temperature and pressure effects on respiration of thecosomatous pteropods. *Deep-Sea Research*, 20, 853-858

Steinacher M., Joos F., Frölicher T. L., Plattner G., Doney S. C. 2009. Imminent ocean acidification in the Arctic projected with the NCAR global coupled carbon cycle-climate model. *Biogeosciences*, 6, 515–533, doi:10.5194/bg-6-515-2009

Stepien J.C. 1980. The occurrence of chaetognaths, pteropod and euphasiids in relation to deep flow recersals in the Straits of Florida. *Deep-Sea Research*, 27A, 987-1011

Taylor J.R. 1996. An Introduction to Error Analysis: The Study of Uncertanties in Physical Measurements. University Science Books, 2nd edition (August 1, 1996), 166-167

Van der Spoel, S. 1967. Euthecosomata: A Group with Remarkable Developmental Stages (Gastropoda, Pteropoda). J. Noorduijn en Zoon N.V., *Gorinchem*, 1-375

Tsurumi M., Mackas D.L., Whitney F.A., DiBacco C., Galbraith M.D., Wong C.S. 2005. Pteropods, eddies, carbon flux and climate variability in Alaska Gyre. *Deep-Sea Research II*, 52, 1037-1053

Ward P., Whitehouse M., Brandon M., Shreeve R., Woodd-Walker R. 2003. Mesozooplankton community structure across the Antarctic Circumpolar Current to the north of South Georgia: Southern Ocean. *Marine Biology,* 143, 121–130

Wells F.E. 1976. Seasonal patterns of abundance and reproduction of euthecosomatous pteropods off Barbados, West Indies. *Veliger*, 18, 241-248

Widdicombe S., Spicer J.I. 2008. Predicting the impact of ocean acidification on benthic biodiversity: What can animal physiology tell us?. *Journal of Experimental Marine Biology and Ecology,* 366, 1-2: 187-197

Wormuth J.H. 1981. Vertical distributions and diel migrations of Euthecosomata in the northwest Sargasso Sea. *Deep Sea Research Part A*, Oceanographic Research Papers, 28, 12: 1493-1515

Yin J., Overpeck J.T., Griffies S.M., Hu A., Russell J.L., Stouffer R.J. 2011. Different magnitudes of projected subsurface ocean warming around Greenland and Antarctica. *Nature Geoscience, Letters*, advance online publication, doi: 10.1038/NGEO1189

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS AND SYMBOLS

APF = Antarctic Polar Front

Chl-a = Chlorophyll a

DGOM = Dynamic Green Ocean Model

DVM = Diel vertical migration

ETP = Eastern Tropical (North) Paficific

ESSD = Earth System Science Data

GLOBEC = GLOBal ocean ECosystems dynamics

MAREDAT = MARineEcosystem DATabase

NetCDF = Network Common Data Form

NH = Northern Hemisphere

OMZ = Oxygen Minimum Zone

PFT = Phytoplankton Functional Type

SH = Southern Hemisphere

DW = Dry Weight

WW = Wet Weight

L = Length

TC = Total Carbon

TIC = Total Inorganic Carbon

TOC = Total Organic Carbon

Ω_{ara} = Aragonite saturation state

$CaCO_3$ = Calcium carbonate

CO_2 = Carbon dioxide

O_2 = Oxygen

1 INTRODUCTION

1.1 The Background – Ocean-atmosphere feedback loops and increasing carbon dioxide concentrations

Human population currently produces large amounts of carbon dioxide (CO_2) through various activities, such as burning of fossil fuels, deforestation, agriculture and cement production (Sabine C.L. et al., 2004). The level of CO_2 before industrial revolution was approximately 280 ppm and has until present day risen to approximately 380 ppm (Feely R.A. et al., 2004; IPCC, 2007). Due to the increased CO_2 (and other greenhouse gasses), the planet is warming and a large portion of excessive heat is being stored in oceans (IPCC, 2007; Gruber N., 2011). Furthermore, the world oceans are the largest carbon reservoirs on earth, removing substantial amount of anthropogenic carbon dioxide produced annually (Sabine C.L. et al., 2004; Khatiwala S. et al., 2009). In the last 250 years, the oceans have taken up approximately one third of all released anthropogenic CO_2 emissions, thus decreasing the rate of global climate change (Sabine C.L. et al., 2004; Sabine C.L. and Feely R.A., 2007). Production and dissolution of oceanic carbonate ($CaCO_3$) by calcifying organisms, like calcifying plankton including coccolithophors, foraminifers and pteropods, have a major influence on the capacity of the oceans to absorb excess atmospheric CO_2 (Fabry V.J., 1989; Doney S.C. et al., 2009). After the die-off of the calcifying plankton their carbonate skeletons sink into deeper water layers where they either dissolve or accumulate in the deep ocean sediments (Fabry V.J., 1989; Tsurumi M. et al., 2005). Not only the sediments, but also the $CaCO_3$ structures in the mid-water layers are a source of carbonate ions that neutralize CO_2, which has been diffused into the surface layers of the oceans and then eventually mixed into deeper waters (Byrne R.H. et al., 1984; Fabry V.J., 1989).

Oceanic continuous uptake of an excess of anthropogenically produced CO_2, combined with ocean warming is predicted to cause major changes in seawater chemistry: pH and carbonate ion decrease, resulting in the shoaling of $CaCO_3$ saturation horizons as well as a decrease in oxygen (O_2) concentration (Feely R.A. et al., 2004; Orr et al., 2005; Fabry V.J. et al., 2008; Widdicombe S. and Spicer J.I., 2008; Keeling R.F., 2010). The ocean pH already declined by 0.1 units since pre-industrial times and is predicted to fall another 0.3 units until 2100 (Caldeira K. and Wickett M. E., 2003). Combined effects of decreasing O_2 levels, changes in temperature and ocean acidification may affect marine biota profoundly, in the long term resulting in changes in biodiversity, trophic interactions and various marine biogeochemical processes, such as ocean carbon cycle (Orr et al., 2005; Fabry V.J. et al., 2008). Among first to be affected are calcifying marine organisms (Orr et al., 2005; Fabry V.J. et al., 2008; Widdicombe S. and Spicer J.I., 2008; Byrne M., 2011), resulting in the biogeochemical changes ultimately affecting the function of the ocean as a carbon sink (Pinsonneault A.J. et al., 2012). It is thus of absolute importance to understand biological responses of marine organisms to elevated partial pressure of CO_2 (pCO_2) levels, reduced pH and $CaCO_3$ saturation as well as possible synergetic impacts of ocean acidification, warming, deoxygenation and other anthropogencally induced changes in the oceans (Hoffman G.E. and Todgham A.E., 2010; Pörtner H.-O. 2008, 2010; Byrne M., 2011; Maas A.E. et al., 2012a).

1.2 Ocean modelling and PFTs

Global ocean biogeochemistry models are used to represent and study the processes in the marine ecosystems. They have been essentially developed on geochemical data on basic physical and chemical variables (e.g. temperature, salinity, nutrient concentration, alkalinity, dissolved oxygen, pH), but in the models of the new generation a wider range of marine ecosystem components is included in the model scheme, as the ocean chemistry is strongly influenced by the activity of various types of plankton (Le Quéré C. et al. 2005, 2009). Incorporating various types of plankton on the base of their functionality enables a better representation of ecosystem functioning (Le Quéré C. et al. 2005, 2009; Hood R.R. et al., 2006). To reduce the biological complexity to a manageable modelling level (Le Quéré C. et al., 2005), the plankton organisms are divided into groups according to their size, function in the food webs and specific function in biogeochemical cycles (e.g. calcification, nitrogen fixation, DMS production) in the marine ecosystems (Hood R.R. et al., 2006; Le Quéré C. et al., 2009). These groups are called Plankton Functional Types (PFTs) and the models incorporating the groups are called the Dynamic Green Ocean Models (DGOMs) (Anderson T.R., 2005; Le Quéré C. et al. 2005, 2009; Hood R.R. et al., 2006).

By incorporating PFTs into biogeochemical models, the understanding of the marine ecosystem dynamics can be improved (Hood R.R. et al., 2006; Le Quéré C. et al., 2009). Furthermore, as the DGOMs take into account the interactions between climate and marine ecosystems, many important scientific questions about functioning of the earth can be addressed (Le Quéré C. et al., 2005). DGOMs are used to study the feedbacks between climate and ocean biogeochemistry and were originally built to help to understand how the marine systems respond to the climate change and how the ocean biochemistry, in particular how biological feedback controls may modulate that change (Le Quéré C. et al. 2005, 2009).

1.3 Research problem

There are still many gaps in the knowledge about the structure and functioning of marine ecosystems, therefore development, parameterization and validation of complex biogeochemical/pelagic ecosystem models presents a major challenge (Hood R.R. et al., 2006). A sufficient amount of observational and experimental data about the ecology, physiology, abundance, biomass and distribution of organisms belonging to individual PFT is necessary to parameterize and to further validate the models (Le Quéré C. et al., 2009). Experimental data describing the functional responses of PFTs to (changing) environmental factors (temperature, light, food concentration) are important particularly in case of modelling marine ecosystem responses to climate change (Le Quéré C. et al., 2009). However, the range and availability of observational and experimental data for many PFTs is currently not sufficient (Hood R.R. et al., 2006; Le Quéré C. et al., 2009). For example, the current representation of calcifying PFTs such as pteropods in large-scale biogeochemical models is still incomplete also due to a substantial lack of information about population dynamics, calcification rates and budgets etc. that would enable incorporation of these groups into models (Hood R.R. et al., 2006).

1.4 General aims - MAREDAT initiative

Among the most important data required to build and evaluate DGOMs is the global and regional carbon biomass of the important PFTs for all seasons (Le Quéré C. et al., 2009). The MAREDAT initiative under The Marine Ecosystem Model Inter-comparison Project (MAREMIP), which promotes the development of models based on PFTs, aims towards building the world atlas of marine plankton functional types. The collective effort is currently being done to assemble the available observation-based data on major PFTs abundance and biomass to form a collection of data sets of selected PFTs (Buitenhuis E.T. et al, 2012a). These data sets will be combined in a common "MARineEcosystem DATa base" (MAREDAT). All the datasets (in NetCDF files) will be publicly available online on PANGEA archives that will serve for future development of models simulating ocean changes and ecosystem functioning and for model validation, with regular update and improvement. The other aim of the MAREMIP is also to promote the interactions between modellers and the scientists doing the observational and experimental work to facilitate future research guidelines, thereby obtaining much needed data through the experiments and observation (Le Quéré C. et al. 2005, 2009; MAREMIP, 2012).

1.5 Specific aims and objectives

The aims of this thesis coincided with the general aims of the MAREDAT initiative since the research work done for this thesis was performed as part of a contribution to MAREDAT global ocean database. The research in this study focuses exclusively on pteropods, one of the PFTs considered important and thus to be represented in DGOMs (Hood R.R. et al., 2006).

The main aim was to gather all currently available observational data on abundance and carbon biomass of pteropods in the world oceans to represent pteropods as a PFT. Using statistical analyses, pteropod global biomass distribution and their contribution to global carbon biomass were obtained. Furthermore, the analyses indicated where future observations should be more in place to fill the gaps in currently lacking knowledge about pteropods. In larger perspective, the created dataset of pteropod abundance and biomass data will provide a tool for more reliable and efficient validation of DGOMs.

As the pteropods represent a diverse group of animals, including multiple species on different trophic levels, they have species-specific responses to various environmental factors, making the task of incorporating them into models even more complex (Hood R.R. et al., 2006). Therefore, an additional aim of this study was to provide an insight into pteropod physiology, their responses, adaptations and bottlenecks under various environmental conditions. Data on physiology would be combined in a dataset, presenting a pre-basis for modelling work. Furthermore, the impact of three main environmental stressors driven by the climate change – ocean warming, acidification and deoxygenation, on pteropods would be assessed.

The results of this research were also used in the scientific research paper which was recently published in Earth System Science Data (ESSD) special issue: MAREDAT – Towards a world atlas of marine plankton functional types (Editors: W. Smith and S. Pesant). This ESSD special issue includes eleven scientific papers presenting eleven abundance datasets and based on that, the global carbon biomass estimations of the

major PFTs recognised to be important in DGOMs (Buitenhuis E.T. et al., 2012a). The summary of the findings of all the papers is gathered in Buitenhuis E.T. et al. (2012a). Our published article is attached at the end of this thesis (Annex D) and can be downloaded from the ESSD website (http://www.earth-syst-sci-data.net/4/167/2012/essd-4-167-2012.html).

2 LITERATURE REVIEW

In the literature review, the ecological and biogeochemical role of pteropods in the marine ecosystems is presented through: 1) description of their known morphology, physiology, biology, 2) their involvement in the biogeochemical cycles and trophic systems and 3) their responses to the environmental conditions (biotic and abiotic environmental factors). In this way I try to demonstrate that the pteropods are one of the important PFT groups and should thus be incorporated into Dynamic Green Ocean Models (DGOMs), and in the MAREDAT project.

2.1 Plankton Functional Types (PFTs)

Different classifications of PFTs are possible, depending on scientific questions addressed and the availability of information on a certain group of organisms (Le Quere et al. 2005, 2009). As a result, the relevance of some groups could be reconsidered after more knowledge on the groups is obtained (Le Quere et al., 2005). PFTs have no phylogenetic meaning, but are composed of many different species with common biomgeochemical functions (Hood R.R. et al., 2006). Some of the major PFTs that are currently recognized and implemented in DGOMs (and are also the groups included in the MAREDAT project) are the following:

- Autotrophic PFTs:
    - Diazotrophs (cyanobacteria - marine N_2 fixers; Luo Y.W. et al., 2012),
    - Diatoms (phytoplankton – O_2, carbon and silica producers; Leblanc K. et al., 2012),
    - Picophytoplankton (the smallest class of phytoplankton, < 2/3 μm in diameter, a diverse group of prokaryotes and eukaryotes; Buitenhuis E.T. et al., 2012b),
    - Coccolithophores (calcifying phytoplankton, also producers of DMSP; O'Brien C. J. et al., 2012),
    - *Phaeocystis (*phytoplanktonic carbon and DMSp producers; Vogt M. et al., 2012).

- Heterotrophic PFTs:
    - Macrozooplankton (zooplankton > 2 mm - holoplanktic and meroplanktic members of the ctenophores, cnidaria, gastropoda, heteropoda, pteropoda, chaetognatha, polychaetea, amphipods, stomatopods, mysids, decapods, and euphausiids; Moriarty R. et al., 2012),
    - Mesozooplankton (200 μm to 2 cm - mainly crustacean plankton, meroplanctic larvae and gelatinuous zooplankton; Moriarty R. and O'Brien T.D., 2012),
    - Foraminifers (calcifying mesozooplankton; Schiebel R. and Movellan A., 2012),
    - Bacteria (pico-heterotrophic degraders of detritus; Buitenhuis E.T. et al., 2012c).
    - Pteropods (holoplanktonic aragonite shell producing gastropods; Bednaršek N. et al., 2012c).

Together with foraminifers and coccolithophores, (euthecosomatous) pteropods are an important group of calcifying planktonic organisms in marine ecosystems, due to their ecological and biogeochemical role (Fabry V.J., 1989; Lalli C.M. and Gilmer R.W., 1989; Hood R.R. et al., 2006; Doney S.C. et al., 2009).

2.2 Description of pteropods

2.2.1 Taxonomy

Pteropods are a group of gastropod molluscs that adopted entirely pelagic life cycle (Hunt B.P.V. et al., 2008). Pteropods are divided into two orders, the Thecosomata (shelled pteropods) and Gymnosomata (naked pteropods) (Lalli C.M. and Gilmer R.W., 1989). The thecosomes and gymnosomes differ in their morphology, behaviour and trophic position. The order of Thecosomata is further divided into suborders Euthecosomata and Pseudothecosomata, which have different anatomical characteristics. The species classification in the order of Thecosomata (Figure 2) is based on their shell morphology whereas for shell-less Gymnosomata (Figure 1) species it is based on the anatomical features of the feeding apparatus (Van der Spoel S., 1976; Lalli C.M. and Gilmer R.W., 1989). Until now 34 euthecosome pteropod species were recognized (Bernard K.S., 2006). Recent genetic studies of pteropods suggested that some taxonomic revisions are required for previously grouped species, due to the new findings based on genetic analysis (Hunt B. et al., 2010; Jennings R.M. et al., 2010), such as a significant genetic variation within same species collected from different geographic regions (Jennings R.M. et al., 2010). The taxonomy of pteropods, including families and species, is presented in the taxonomic tree in Figure 3.

2.2.2 Shell morphology and movement

Thecosomes produce external calcium carbonate shells, the morphology of the which is very diverse (Gilmer R.W. and Harbison G.R., 1986; Sato-Okoshi W. et al., 2010), ranging from globular and spirally coiled (genus *Limacina*), or bilaterally symmetrical (family Cavoliniidae), the latter being either conical and pointed (genus *Creseis*), bottle-shaped (genus *Cuvierina*) or pyramidal (genus *Clio*) (Gilmer R.W. and Harbison G.R., 1986; Lalli C.M. and Gilmer R.W., 1989; Sato-Okoshi W. et al., 2010; Annex A). Gymnosomes only have a large shell (presumed to be aragonite) in their veliger life stage that is cast off at metamorphosis (Fabry V.J. et al., 2008). Pseudothecosomatous pteropods also possess a veliger shell, which they discard at metamorphosis to gelatinous and shell-less adults (Fabry V.J. et al., 2008). Gymnosomes and pseudothecosomes are shell-less during most of their life time.

Both groups of pteropods swim by flapping their wing-like parapodia (swimming wings) that evolved from the original gastropod foot (Lalli C.M. and Gilmer R.W., 1989; Seibel B.A. et al., 2007). Euthecosomes have parapodial wings and pseudothecosomes often have parapodia fused into a swimming plate (Gilmer R.W. and Harbison G.R., 1986). Gymnosomes have muscular paired parapodia, usually a very well-defined head, tough and elastic body cover and specialised feeding organs differing greatly between different species (Lalli C.M. and Gilmer R.W., 1989).

Pteropods are a group of marine gastropods variable in sizes (Annex A), but generally gymnosome species can achieve bigger sizes (e.g. *Clione limacina* can grow up to 50 mm; Böer M. et al., 2005) than thecosomatous species (e.g. *Limacina helicina* can grow up to 12 mm; Lalli C.M. and Wells F.E., 1978 cited in Gannefors C. et al., 2005). Sizes of adult specimen belonging to the same species can differ between individuals from different regions and through different seasons (Kobayashi H.A., 1974; Gilmer R.W. and Harbison G.R., 1991; Gannefors C. et al., 2005).

***Figure 1**: Gymnosomatous pteropod Clione limacina, Kevin Raskoff (Hidden Ocean 2005 Expedition: NOAA Office of Ocean Exploration, expl0391, Voyage To h NOAA Collext.xploring the Seas With NOAA Collect. http://www.photolib.noaa.gov/htmls/expl0391.htm, accessed 20.11.2012).*

***Figure 2**: Thecosomatous pteropod Limacina helicina, Erling Svenson (Gannefors C. et al., 2005: 170)*

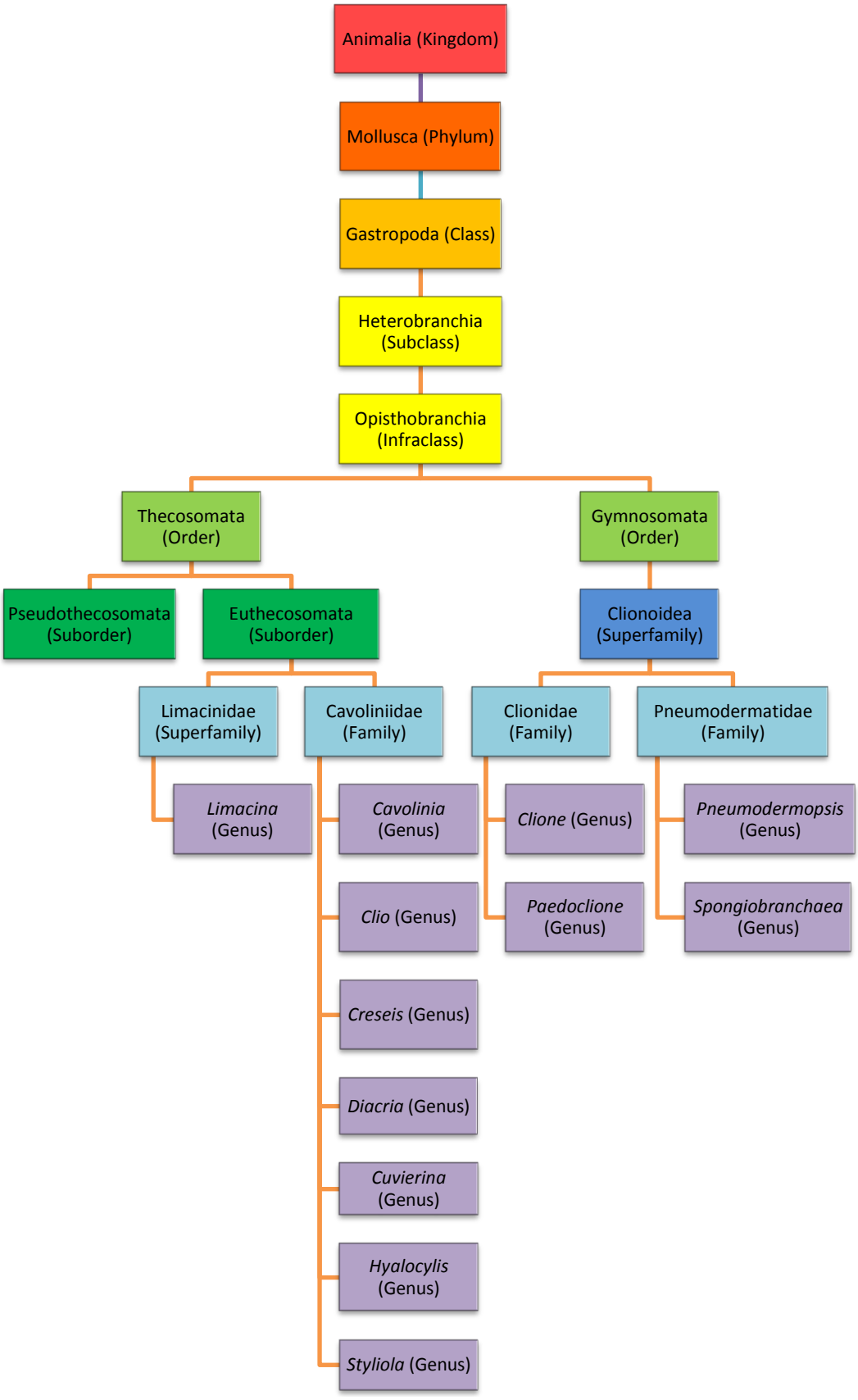

***Figure 3**: Taxonomy tree of pteropods*

The active swimming of thecosomes appears to be mainly used for avoiding predation (Harbison G.R. and Gilmer R.W., 1992) and for conducting diurnal vertical migrations, as swimming is an energetically costly activity (Lalli C.M. and Gilmer R.W., 1989). They remain motionless during feeding and retain neutral buoyancy by extending deployment of mucous web used for feeding (Gilmer R.W. and Harbison G.R., 1986; Lalli C.M. and Gilmer R.W., 1989; chapter 2.2.4). Gilmer R.W. and Harbison G.R. (1986) observed that thecosome pteropods were either neutrally buoyant (*Cavolinia* spp.*, Diacria* spp.) or sink very slowly (*Cuvierina* spp.*, Clio* spp.*, Hyalocylis* spp.*, Styliola* spp.*, Creseis* spp.*, Limacina* spp.) even when they were not feeding. Seibel B.A. et al. (2007) determined the relative densities of thecosome species *Limacina helicina* and gymnosome *Clione antarctica*, whereby *Limacina helicina* was negatively and *Clione antarctica* was nearly neutrally buoyant relative to the sea water in McMurdo Sound.

2.2.3 Formation and function of the aragonite shell

Euthecosomatous pteropods form shells made of aragonite, which is a metastable polymorph of $CaCO_3$ and is approximately 50% more soluble in seawater than calcite (Mucci A., 1983). Therefore, pteropod shells are very sensitive to dissolution (Orr C.J. et al., 2005; Fabry V.J. et al., 2008; Comeau S. et al. 2010a, 2010b; Lischka S. et al., 2011; Bednaršek N. et al., 2012b). Beside coccolithophores and foraminifers, euthecosomes are the major marine planktonic $CaCO_3$ producers and the only major planktonic aragonite producers, as the coccolithophores and foraminifers produce calcite shells instead (Hood R.R. et al., 2006; Fabry V.J. et al., 2008; Doney S.C. et al., 2009). In tropical and subtropical regions, two families of holoplanktonic heteropods also posses aragonite shells (Fabry V.J. et al., 2008). Even though pteropods account for a smaller fraction (10%-35%; Fabry V.J., 1990; Gangstø R. et al., 2008) of total global $CaCO_3$ production, they can contribute a substantial part on regional levels and on the specific temporal scales (Fabry V.J., 1989; Accornero A. et al., 2003; Fabry V.J. et al., 2008).

Pteropods construct their shells in the same way as other molluscs (Bandel K., 1982 cited in Bandel K. and Hemleben C., 1995; Lalli C.M. and Gilmer R.W., 1989). The shell of adult *Limacina helicina* is constructed from three layers - a crossed-lamellar layer formed from aragonite, considered to be absorbed from surrounding seawater, situated between very thin outer (periostracum) and thicker innermost prismatic layer, both formed from organic materials the source of which are the soft tissues (Sato-Okoshi W. et al., 2010; Bednaršek N. et al., 2012c). However, the shell structure, thickness and shape were observed to vary between Arctic and Antarctic *Limacina helicina* and between shells of different life stages (Sato-Okoshi W. et al., 2010). Although the shell of *Limacina helicina* is among the thinnest (2-9 μm) observed for shelled gastropods and thus the effectiveness of this shell as a defence against predators is doubtful, it combines elasticity and strength due to its multilayered structure, with a potential to endure a certain measure of chemical dissolution and mechanical degradation (Sato-Okoshi W. et al., 2010). A thin shell represents an evolutional advantage for the pelagic life of pteropods due to its lightness, increasing buoyancy and less materials and energy required for its construction (Lalli C.M. and Gilmer R.W., 1989; Sato-Okoshi W. et al., 2010). The larger species belonging to the family Cavoliniidae possess thicker (100 μm) shells, with different internal microstructure (Lalli C.M. and Gilmer R.W., 1989).

Several studies indicate that pteropods demonstrate reduced calcification rates and increased dissolution of aragonite shells when exposed to elevated pCO_2 and decreasing pH and CO_3^{2-} concentrations (Feely R.A. et al., 2004; Orr C.J. et al., 2005; Fabry V.J. et al., 2008; Comeau S. et al., 2009; Bednaršek N. et al., 2012a; chapter 2.6.2). Environmental factors such as temperature, salinity and possibly food abundance strongly influence the growth, structure and morphology of the pteropod shell (Schalk P.H., 1990; Sato-Okoshi W.

et al., 2010; chapter 2.4.1). Upon observations Juranek L.W. et al. (2003) suggested that majority of calcification in certain species probably occurs during the day, when populations occupy deeper water layers due to their diel migration behaviour (Wormuth J.H., 1981; chapter 2.2.6) rather than at night, when residing near/at the surface. The adaptive value of this trend is unknown as the reduced aragonite saturation state and colder temperatures in deeper water layers make shell formation there energetically more expensive and slow (Juranek L.W. et al., 2003). One explanation for deeper water calcification could be that it is not primarily related to aragonite saturation rates, but that the depth and the timing of calcification are more strongly related to other abiotic and biotic factors influencing their diel migrations, such as temperature, light intensity, food availability and predator avoidance (Juranek L.W. et al., 2003). Seasonal calcification depths of *Styliola subula* and *Limacina helicina* were observed to be shallower in the summer/autumn and deeper in the winter/spring in Sargasso Sea, thus possibly a response to seasonal hydrographic changes (thermal stratification) in the water column (Juranek L.W. et al., 2003). Furthermore, pteropods were after all observed to be also able to precipitate $CaCO_3$ in aragonite undersaturated ($1> \Omega_{ara}$) conditions, although the growth rates were reduced (Comeau S. et al., 2010a; Lischka S. et al., 2011).

2.2.4 Feeding biology

Thecosomes capture food using a spherical (euthecosomes) or funnel shaped (pesudothecosomes) mucous webs several times the size of their body, which are suspended above the animals during feeding (Gilmer R.W. 1972, 1990; Gilmer R.W. and Harbison G.R., 1986). Thecosomes are extremely sensitive to turbulence and will discard or instantly ingest (some pseudothecosomes) their nets and rapidly escape by swimming away, if disturbed (Gilmer R.W. and Harbison G.R., 1986; Gilmer R.W., 1990). They use no active transport of water through the web and do not move during feeding (Gilmer R.W., 1990). Thecosomes are omnivores consuming the prey of all sizes (Gilmer R.W., 1990). After they withdraw the web, they consume it together with the captured prey, which is a combination of trapped motile organisms such as protozoans and zooplankton and collected sinking particles (Gilmer R.W., 1990; Gilmer R.W. and Harbison G.R., 1991). Food preference of pteropods depends on the food availability (opportunistic feeding) and the size of individuals (Gilmer R.W. and Harbison G.R., 1991; Gannefors C. et al., 2005; Annex B). Consequently their dominant food source can change according to their life stage – their ability to handle larger pray increases with their size, therefore smaller specimen often rely on particulate organic matter (e.g. juvenile *Limacina helicina* in Arctic; Gannefors et al. 2005; Kobayashi H.A., 1974) or are herbivorous, but switch to omnivory at larger sizes (Gilmer R.W. and Harbison G.R., 1991; Gannefors C. et al., 2005). However, based on the results of the faecal pellet composition of *Limacina helicina* (from the Ross Sea, Antarctica) it was suggested, that also many smaller pteropod specimen were omnivores (Manno C. et al., 2010). Thus, according to Manno C. et al. (2010), *Limacina helicina* is a true omnivore, feeding on available particulates and is not an opportunistic omnivor only at larger sizes as suggested by Gilmer R.W. and Harbison G.R. (1991). In addition, diet can change seasonally depending on available food sources; the diet of the Arctic *Limacina helicina* was observed to range from phytoplankton dominated diet in spring and summer to feeding on degraded organic material in late autumn and winter (Gannefors C. et al., 2005). Additionally, there was an even more subtle variation in phytoplankton-dominated diet of *Limacina helicina* during spring/summer period – diatom-dominated in spring and changed to dinoflagellates in summer/autumn (Gannefors C. et al., 2005). Juvenile *Limacina helicina* were reported to rely on particulate organic matter originating from the Arctic sea ice (Gannefors C. et al., 2005; Kobayashi H.A., 1974). Finnaly, Gilmer R.W. and Harbison G.R. (1991) reported a considerable part of the *Limacina helicina* diet in mid-summer consisted of zooplankton and juvenile *Limacina helicina*. Thecosomatous pteropods thus show opportunistic behaviour in their range of food sources, with further tendency to respond to the sudden increase in food

supply in the environment (a phytoplankton bloom), which results in a dramatic increase in pteropod population size (Wormuth J.H., 1985).

Gymnosomes are highly specialized carnivorous predators (Lalli C.M. and Gilmer R.W., 1989; Seibel B.A. and Dierssen H.M., 2003; Seibel B.A. et al., 2007). The diet is only known for a selection of gymnosome species and all of them feed exclusively on thecosomes: *Clione limacina* feeds on *Limacina helicina* in polar and on *Limacina retroversa* in temperate waters (Lalli C.M. and Gilmer R.W., 1989), whereas *Spongiobranchea australis* feeds on *Clio pyramidata* (Hunt B.P.V. et al., 2008). However, the earliest larval stages of *Clione limacina* feed on phytoplankton, although very soon they become predaceous feeders (Mileikovsky S.A., 1970). Gymnosomes evolved their feeding structures to extract thecosomes out of their shells, the hunting techniques to catch them efficiently and highly efficient digestion and assimilation of their prey (Lalli C.M. and Gilmer R.W., 1989). It was the coevolution of the prey and predator (Seibel B.A. et al., 2007). *Clione limacina* feeds on *Limacina helicina* even during its very early larval stages (Conover R.J. and Lalli C.M., 1972; Lalli C.M. and Gilmer R.W., 1989). This food dependence of gymnosomes on their only prey may result in long periods of starvation when the single food source is scarce, resulting in some adaptations to such life style (Böer M. et al., 2005); the species *Clione limacina* developed a various extraordinary life-strategies, such as body shrinkage, utilisation of body constituents not essential for survival (e.g. gonads), low metabolism, specialisation in lipid biosynthesis and the slow lipid consumption, to cope with the food limitation (Böer M. et al. 2005, 2007). Specimen of *Clione limacina* (collected in the Svalbard, Arctic) survived in an aquarium for nearly a year without food (Böer M. et al., 2007).

2.2.5 Life cycle and reproduction

The reproductive biology of thecosomes and gymnosomes is relatively well studied (described in details in Lalli C.M. and Gilmer R.W., 1989). Reproduction is closely corresponding to seasons, with one or two generations per year and is correlated with favourable environmental conditions such as food abundance.

Common reproductive characteristics of thecosomes include the majority of species being protandrous hermaphrodites - first functioning as males and secondarily as females, which is coinciding with degeneration of male reproductive organs (Lalli C.M. and Gilmer R.W., 1989). Gymnosomes on the other hand may function as simultaneous hermaphrodites at maturity, meaning that male reproductive organs do not degenerate in females (Lalli C.M. and Gilmer R.W., 1989; Hunt B.P.V. et al., 2008).

Mature females produce eggs (Lalli C.M. and Gilmer R.W., 1989; Gannefors C. et al., 2005) and generally most of them die shortly after the spawning (Kobayashi H.A., 1974; Wells F.E., 1976; Dadon J.R. and de Cidre L.L., 1992; Gannefors C. et al., 2005), although some females can also survive until the next spawning (Gannefors C. et al., 2005). The veligers hatch within 2-6 days after spawning and start feeding immediately (Lalli C.M. and Gilmer R.W., 1989) and utilizing the food for growth and accumulation of necessary lipids (Gannefors C. et al., 2005). To develop into mature females, juveniles require continuous input of food (Gannefors C. et al., 2005). Bandel K. and Hemleben C. (1995) research on thecosomatous species confirmed that the general features of their early development do not deviate from those of the other marine gastropods in any essential ways. However, much less research was done on life cycles, life spans, growth rates and times of spawning of pteropods and only for certain species. For many pteropod species no data is available as for the others the research conducted often resulted in different suggestions about the life cycles and life spans of pteropods. An example is the life expectancy of pteropod *Limacina helicina,* one of the most studied pteropod species. Kobayashi H.A. (1974) suggested a 1.5-2 year life span for *Limacina helicina* in the Arctic Ocean. Bednaršek N. et al. (2012a) on the other hand

proposed a 3< year life span for *Limacina helicina antarctica* in Scotia Sea (Antarctica), whereas according to Hunt B.P.V. et al. (2008) *Limacina helicina antarctica* lives for one year in the Southern Ocean. Fabry V.J. (1989) and Gannefors C. et al. (2005) also proposed a year long life cycle for *Limacina helicina* in the Arctic. Van der Spoel S. (1973) and Wells F.E. (1976) suggested only one year life span for *Limacina helicina* and also for several other pteropod species. In addition, a research was carried out for gymnosome *Clione limacina*, estimating at least a 2 year-life cycle (Böer M. et al., 2005). Clearly, there is still the need for more research due to the lack (for gymnosomes) or great diversity (for *Limacina* spp.) in observations done until now.

Some pteropod species were observed to have a life cycle of two generations per year (Dadon J.R. and de Cidre L.L., 1992; Gannefors C. et al., 2005). In the Argentine Sea, *Limacina retroversa* exhibited a two generation annual cycle (Dadon J.R. and de Cidre L.L., 1992). The first breeding event in early spring produced offsprings that took the advantage of favourable environemtnal conditions and matured early so as to breed in summer and produce the second generation, which overwintered, reaching sexual maturity after the winter and breeding again in the following spring (Dadon J.R. and de Cidre L.L., 1992). However, *Clione limacina* was observed to spawn throughout the whole year, although with lower intensity in autumn/winter period (Mileikovsky S.A., 1970). Similarly, *Cuvierina columnella* in Sargasso Sea appeared to reproduce year-round, with slight increase in spring and summer (Almogi-Labin A. et al., 1988). Due to regionally changing environmental conditions, such as fluctuating food availability, which influences pteropod growth and reproduction rates, a regional variability in (max/maturation) size, life cycle and growth rates of pteropods (of the same species) was observed in the Northern Hemisphere (NH), presented in the case of *Limacina helicina* (Kobayashi H.A., 1974; Almogi-Labin A. et al., 1988; Fabry V.J., 1989; Gannefors C. et al., 2005; Bednaršek N. et al., 2012a) and *Clione limacina* (Lalli C.M. and Gilmer R.W., 1989). *Limacina helicina* specimen found in the sub-arctic regions were 2-3-times larger from the specimen of the same species, found in the Arctic (Kobayashi H.A., 1974; Gilmer R.W. and Harbison G.R., 1991; Gannefors C. et al., 2005). Furthermore, northern hemisphere *Clione limacina* was observed to have a positive size correlation with the size of its prey *Limacina* (Conover R.J. and Lalli C.M., 1972). Thus, similar trends of variable sizes and life cycles can probably be expected for the Southern Ocean formae of *Limacina antarctica* and consequently *Clione antarctica*, as the regional changes in environmental conditions are common there as well (Hunt B.P.V. et al., 2008). Moreover, in the Southern Hemisphere (SH) (Sargasso Sea) also a clear seasonality in the maximum adult shell sizes of *Limacina inflata* and *Limacina bulimoides* was exhibited, with largest shells in spring, at the time of highest food availability (Almogi-Labin A. et al., 1988). However, these trends are not necessary to be applicable for all the pteropod species, especially as for some species such as *Clio piatkowskii* and *Spongiobranchaea australis,* no data on life cycles is yet available (Hunt B.P.V. et al., 2008).

2.2.6 Global and vertical distribution

Pteropods are found predominantly in near-surface waters, although deep sea species (living at least part of their life time deeper than 1000 m; Wormuth J.H., 1981) are also known to exist (Lalli C.M. and Gilmer R.W., 1989; Hunt B.P.V. et al., 2008), such as thecosome *Limacina helicoides,* considered to be a bathypelagic species occurring exclusively below 1000 m (Van der Spoel S., 1967).

Shelled pteropods are important components of polar and sub-polar ecosystems (Fabry V.J. et al., 2008). The highest species diversity of euthecosomatous pteropods is found in tropical and subtropical regions (Lalli C.M. and Gilmer R.W., 1989; Fabry V.J. et al., 2008), the highest abundances on the other hand are found at high latitudes (Lalli C.M. and Gilmer R.W., 1989). Tipical tropical euthecosome species are *Cavolinia longirostris, Cavolinia*

uncinata, Creseis acicula, Creseis virgula virgula, Creseis virgula conica, Cuvierina columnella, Diacria quadridentata, Hyalocylix striata, Limacina bulimoides and *Limacina trochiformis* (Solis N.B. and von Westernhagen H., 1978). Two subtropical euthecosome species are *Clio pyramidata* and *Limacina inflata* (Solis N.B., von Westernhagen H., 1978). The only thecosomatous pteropod species found in the Arctic is *Limacina helicina* (Gannefors C. et al., 2005; Comeau S. et al., 2010a). The dominant euthecosome pteropod species in the Southern Ocean are *Limacina retroversa australis* (north of Polar Frontal Zone – predominantly sub-Antarctic species), *Limacina helicina antarctica* (south of the Polar Frontal Zone), *Clio pyramidata sulcata* (waters south of the Antarctic Polar Front) and *Clio piatkowskii* (Boltovsky D., 1999; Hunt B.P.V. et al., 2008).

Some pteropod species, like thecosome *Limacina helicina helicina* and gymnosome *Clione limacina*, were proposed to have a bipolar distribution (Van der Spoel S., 1976; Van der Spoel S. and Dadon J.R., 1999) The results of the recent study by Jennings R.M. et al. (2010) confirmed *Limacina helicina helicina* found in separate regions of NH (Princ William Sound and the Arctic) to be genetically similar. However, *Limacina helicina helicina* and *Limacina helicina antarctica* turned out to be genetically strongly differentiated, with differences more typical for separate pteropod species (Jennings R.M. et al., 2010). Similarly, Hunt B. et al. (2010) stated, based on the results of the genetic analysis, that *Limacina helicina* is in fact not bipolar, but that the Arctic and Antarctic populations differ at the species level and are not different subspecies (*Limacina helicina helicina* and *Limacina helicina antarctica*, respectively) as listed currently. The other pteropod species, such as *Cavolinia uncinata, Clio cuspidata, Cuvierina columnella* and *Diacria major* also appear in far-distanced regions, yet the populations are genetically different (Jennings R.M. et al., 2010). The taxonomy status of certain pteropod species such as of *Limacina helicina* group remains to be fully resolved through further phylogeographic analysis (Hunt B. et al., 2010; Jennings R.M. et al., 2010).

Pteropod *Clione limacina* is the most abundant gymnosome of the pelagic food web in temperate and polar waters (Böer M. et al., 2005). Its distribution is bipolar (latitudes poleward of 40° in NH and SH), although the northern and southern populations are hypothesized to be distinct subspecies (*Clione limacina limacina* and *Clione limacina antarctica*) or even separate species (*Clione limacina* and *Clione antarctica*) (Mileikovsky S.A., 1970; Van der Spoel S., 1976; Gilmer R. and Lalli C., 1990; Van der Spoel S. and Dadon J.R., 1999; Jennings R.M. et al., 2010). Gymnosome *Spongiobranchea australis* has a circumantarctic distribution (Jennings R.M. et al., 2010). *Clione limacina antarctica* and *Spongiobranchaea australis* are the dominant gymnosomes in the Southern Ocean (Hunt B.P.V. et al., 2008).

The majority of euthecosome pteropod species exist in the surface layers, down to approximately 200 m, although mesopelagic and bathypelagic species also occur (Van der Spoel S., 1967; Wormuth J.H. 1981, 1985). According to studies of Myers T.D. (1968) and Haagensen D.A. (1976) cited in Stepien J.C. (1980) most pteropod species are predominantly epipelagic (occurring in the upper 200 m), some however are diurnal migrators from epipelagic to mesopelagic zone (Stepien J.C., 1980). Due to the downward water currents (downwelling of shallow ocean waters), epipelagic pteropod species can be carried to unusual depths, which happened in the Florida Straits of Miami, where non-migratory epipelagic pteropod species (*Limacina trochiformis, Creseis virgula)* in combination with mesopelagic pteropods were recorded below 600 m (Stepien J.C., 1980).

Several pteropod species including thecosomes, such as *Limacina* spp*., Clio pyramidata, Styliola subula,* as well as gymnosomes, such as *Clione limacina antarctica,* were observed to be diel vertical migrators, moving closer to the surface (usually in the upper 100 m) reach in food during the night and retreating to greater depth during the day (Wormuth J.H., 1981; Mackas D.L. and Galbraith M.D., 2002; Hunt B.P.V. et al., 2008; Flores H. et al., 2011). Non-

migratory or feebly migratory thecosome species limited primarily to the upper 100 m are *Cavolinia longirostris, Creseis acicula, Creseis virgula* and *Limacina trochiformis* (Meyers T.D., 1968 and Haagensen D.A., 1976 cited in Stepien J.C., 1980), as well as *Diacria rampali* (Andersen V. et al., 1997). Some of the strongly migratory thecosome species living primarily in the mesopelagic zone (100-600 m) during the day and in the upper epipelagic zone at night are *Clio pyramidata, Cuvierina columnella, Limacina bulimoides, Limacina inflata, Limacina lesueri* and *Styliola subula* (Meyers, 1968 T.D. and Haagensen D.A., 1976 cited in Stepien J.C., 1980; Andersen V. et al., 1997), as well as *Cavolinia inflexa, Diacria trispinosa* and *Clio cuspidata* (Andersen V. et al., 1997).

Some thecosomes can migrate over 350 m on a daily basis (Wormuth J.H., 1981). The migration patterns and ranges differ significantly among various species of pteropods (Wormuth J.H., 1981; Lalli C.M. and Gilmer R.W., 1989), but also with their life-stage and size (Mileikovsky S.A., 1970; Bathmann U.V. et al., 1991). Furthermore, migration and dwelling depth can change with season (Chen C. and Bé A.W.H., 1964; Kobayashi H.A., 1974; Lischka S. et al., 2011; chapter 2.4.2), can be a response to availability of food (Kobayashi H.A., 1974; chapter 2.3.1) or can be predator-avoidance behaviour (Falk-Petersen S. et al., 2008; chapter 2.3.2). Diel vertical migrations (DVMs) of zooplankton are believed to be influenced by the balance between the risk of predation and the necessity of feeding (Gliwicz M.Z., 1986). Ohman M.D. (1990) also pointed out there is an energy cost in performing DVMs and therefore only if there is a significant pressure of predators the cost of DVMs is justified. Seasonal vertical migration is related to the life-cycle strategy of zooplankton organisms and is often associated with feeding in the productive layers during spring and summer and over wintering in cold deep waters (Almogi-Labin A. et al., 1988; Falk-Petersen S. et al., 2008). DVMs of *Clio pyramidata* and *Clione limacina* were even recorded happening under the ice in the Antarctica (Lazarev Sea), from depths in the day into ice-water interface layer during the night, in the summer and winter season (Flores H. et al., 2011). Furthermore, gymnosomes have a very close relationship with their exclusive prey and there is some evidence of vertical distribution of gymnosome *Clione limacina antarctica* tracking that of thecosome *Limacina helicina antarctica* in the East Antarctica and Lazarev Sea (Hunt B.P.V. et al., 2008). Similarly, a remarkable resemblance in distribution patterns of *Clione limacina* and its exclusive prey *Limacina helicina* was observed in the NW Pacific Ocean (Volkov A.F., 2008). More about the DVMs of pteropods and what influences them is explained in chapters 2.4.5 and 2.3.1.

In summary, pteropods have a world-wide distribution, with highest abundances at high latitudes and the greatest species diversity in tropical and subtropical regions. Epipelagic, mesopelagic as well as deep water species exist, among which many exhibit DVMs. The migration patterns and ranges differ among various species and are related to or influenced by different environmental (biotic and abiotic) factors (chapter 2.3.1, 2.3.2, 2.4.5).

2.3 Adaptations and responses of pteropods to biotic factors in the environment

2.3.1 Fluctuations in food availability and food quality

Food availability influences metabolic rates of pteropods, thereby affecting their oxygen consumption, protein synthesis, growth, reproduction and consequently the density of pteropods (Seibel B.A. and Dierssen H.M., 2003; Bernard K.S., 2006; Bernard K.S. and Froneman P.W., 2009; Maas A.E. et al., 2011). Food scarcity can be the cause for delays in spawning and juvenile metamorphosis, in a long term leading to higher population vulnerability (Seibel B.A. and Dierssen H.M., 2003; Böer M. et al., 2006; Bernard K.S., 2006; Bernard K.S. and Froneman P.W., 2009). On the other hand, local favourable food

conditions may result in higher metabolic and reproductive rates of pteropods (Seibel B.A. and Dierssen H.M., 2003; Kosobokova K.N. and Hopcroft R.R., 2010). However, pteropod densities depend not only on quantity, but also on quality of food (Perissinotto R., 1992; Bernard K.S., 2006; Maas A.E. et al., 2011). Pteropods have different strategies to cope with fluctuating food resources, such as migration, utilisation of less essential body constituents or lipids, changing metabolic rates and changing of the food source (Connover R.J. and Lalli C.M., 1974; Gilmer R.W. and Harbison G.R., 1991; Kattner G. et al., 1998; Böer M. et al. 2005, 2007; Seibel B.A. and Dierssen H.M., 2003; Seibel B.A. et al., 2007; Hunt B.P.V. et al., 2008; Maas A.E. et al., 2011).

In the polar environment, high seasonality and often extreme living conditions were strong evolutionary factors for pteropods towards adopting several mechanisms and strategies to be able to survive (Böer M. et al. 2005, 2007; Gannefors et al., 2005; Seibel B.A. et al., 2007; Rosenthal J.J.C. et al., 2012). In the polar environments, such as the Southern Ocean, primary production is strongly related with the seasonally changing extent of the sea ice (Brierley A.S. and Thomas D.N., 2002). Although the sea ice cover can be the cause of a decrease in primary production due to shading of underlying water column, it more often provides protection from surface predators and a source of biogenic material (organic matter, algae inhabiting sea ice) thus representing favourable feeding grounds for zooplankton (Brierley A.S. and Thomas D.N., 2002). In summer, melting sea ice releases particulate organic matter into the water column, thereby supporting the phytoplankton blooms (Brierley A.S. and Thomas D.N., 2002). However, due to the pronounced seasonality in light conditions, temperature and ice cover in the polar regions, blooms of primary producers are short and intensive (Sakshaug E., 2003) and are a major factor influencing pteorpod populations – thecosomes directly and gymnosomes indirectly (thorugh the thecosomes) (Lalli C.M. and Gilmer R.W., 1989; Seibel B.A. and Dierssen H.M., 2003; Bernard K.S., 2006).

Bernard K.S. (2006) reported a positive correlation between total chlorophyll a (chl-a) concentration and *Limacina retroversa* numbers in Polar Frontal Zone (Southern Ocean), which suggested a dependency of the thecosome pteropods on available phytoplankton abundance. When phytoplankton biomass was in decline, the abundance of *Limacina retroversa* was low as well (Bernard K.S., 2006). Similarly, Seibel B.A. and Dierssen H.M. (2003) observed a correlation between reduced phytoplankton biomass in McMurdo Sound (Antarctica) and lower abundance and decreased metabolic rates of *Limacina helicina*, which in turn also impacted the occurrence and metabolic rates of *Clione antarctica,* preying exclusively on *Limacina helicina*. A significantly reduced phytoplankton stocks (50-75% lower chl-a concentrations in comparison with previous years) in McMurdo Sound clearly affected the population of *Limacina helicina*, because the oxygen consumption rates of *Limacina helicina* were reduced and in the following season *Limacina helicina* (for the first time in record) was not found in the McMurdo Sound (Seibel B.A. and Dierssen H.M., 2003). Consequently, the absence of *Limacina helicina* impacted its predator *Clione antarctica*, which was indicated in its lower metabolic rates (Seibel B.A. and Dierssen H.M., 2003). A supportive result of the laboratory experiments demonstrated the metabolic rates of starving *Clione antarctica* to decline (Seibel B.A. and Dierssen H.M., 2003). Supportive findings were also reported by Maas A.E. et al. (2011) – metabolic rates of *Limacina helicina* were depressed at lower mean chl-a concentrations in the Ross Sea. The laboratory incubation of *Limacina helicina* and its predator *Clione limacina antarctica* after 4 days without food also resulted in depressed metabolic rates, 20% and 35%, respectively (Maas A.E. et al., 2011).

Low metabolism, i.e. suppressed oxygen consumption, is a part of a combined strategy of gymnosome *Clione limacina* to survive food scarcity, also including body shrinkage (of all body parts), utilisation of body constituents and organs (e.g. gonads) not essential for survival, and the slow consumption of stored lipids (Conover and Lalli, 1974; Kattner G. et al., 1998; Böer M. et al. 2005, 2007; Seibel B.A. and Dierssen H.M., 2003; Seibel B.A. et al.,

2007; Maas A.E. et al., 2011). Thecosome *Limacina helicina* was also documented to rely on lipid stores in times of food shortage (Gannefors C. et al., 2005; Böer M. et al., 2005). In addition, thecosomatous peropods may switch to a different diet during the food limited periods – during the winter in the absence of phytoplankton blooms they might utilise floating organic particles, switch to carnivory (including cannibalism) and switch back to herbivory in the times of phytoplankton abundance (Gilmer R.W. and Harbison G.R., 1991; Hunt B.P.V. et al., 2008). However, as mentioned before, according to Manno C. et al. (2010), thecosome *Limacina helicina* does not exactly switch between herbivory and omnivory in times of food scarcity (as proposed by Gilmer R.W. and Harbison G.R., 1991), but is omnivory at all time, only its main food source changes due to availability (Manno C. et al., 2010). As a result, *Limacina* has the advantage of being able to successfully respond to changing environment conditions, such asprecipitous declines and sudden blooms in food levels that occur in subarctic and temperate regions. On the other hand, monophagous gymnosomes such as *Clione limacina* clearly rely on their lipid storages instead of alternative external food sources, as in times of starvation they use the lipids otherwise utilised for spawning, maturation and production of gonads for maintaining the basic life functions (Böer M. et al. 2005, 2007). The starvation tolerance of *Clione limacina* is dependent on the ontogenetic stage, reproduction (egg production) and physiological condition of the animals (Böer M. et al., 2006). During a long-term starvation experiment with *Clione limacina*, the sexual regression was observed, pteropod utilizing the gonads as an energy source (Böer M. et al., 2007). A positive correlation between egg production and availability of food in case of *Clione limacina* was demonstrated in the laboratory experiments (Lalli C.M. and Gilmer R.W., 1989). Moreover, the spawning of the gymnosome *Clione limacina* in North Atlantic, Subarctic and the North Pacific Oceans is correlated with the spring/summer period and peak abundance of phytoplankton, which serves as food for the earliest larval stages and early polytrochous larvae (Mileikovsky S.A., 1970; Böer M. et al., 2005). It seems that gymnosomes may be well adapted to starvation, but their survival in a food limited environment can be on the expense of reproduction (Seibel B.A. and Dierssen H.M., 2003).

The correlation between food abundance and reproduction patterns was suggested for thecosome pteropods as well. Bernard K.S. (2006) suggested a possible delay in spawning of *Limacina retroversa* due to the low observed chl-a concentration in Polar Frontal Zone (Southern Ocean). Furthermore, food deprivation caused a delayed reproduction in subpolar *Limacina retroversa* (Böer M. et al., 2006; Bernard K.S. and Froneman P.W., 2009). In general, relatively short delays in food availability are known to lead to failed metamorphosis of larval zooplankton (Ross R.M. and Quetin L.B., 1989 cited in Seibel B.A. and Dierssen H.M., 2003), which could be the case in the McMurdo Sound, where food deprivation of *Limacina helicina* veligers prevented them to grow to adult sizes until the summer, when they could reproduce again (Seibel B.A. and Dierssen H.M., 2003). The competition for food with other zooplankton at times or following the times of high primary production, can also result in high mortality of juvenile pteropods (veligers, larvae), which were produced in great numbers in reproduction response to increase in primary production, but many end up with too little food to survive (Almogi-Labin A. et al., 1988).

Various species adapt their migration patterns in accordance to (seasonal) food availability. Thecosomes and gymnosome larvae (e.g. *Clione limacina*) feeding on phytoplankton migrate into the surface layer in times of high primary production (in spring and summer) (Mileikovsky S.A., 1970; Falk-Petersen S. et al., 2008). Similarly, gymnosomes follow their prey when thecosomes migrate into shallower or deeper waters due to various reasons such as food availability or overwintering (Mileikovsky S.A., 1970; Hunt B.P.V. et al., 2008; Falk-Petersen S. et al., 2008).

Seibel B.A. et al. (2007) proposed a strong correlation of metabolic rates and locomotory capacity of gymnosomatous predators with their thecosomatous prey, correlated with their possible co-evolution hunting mechanisms responding directly to predation avoiding strategy

of the prey. Gymnosome *Cliopsis krohni* feeds predominantly (possibly exclusively) on pseudothecosome *Corolla* spp. (Seibel B.A. et al., 2007). *Corolla* spp. is a slow-moving pteropod and *Cliopsis* spp. hunting technique is accordingly less locomotory demanding than the hunting performed by *Clione limacina,* feeding on faster swimming *Limacina helicina* (Seibel B.A. et al., 2007). Therefore, it makes sense the metabolic rates of less active *Corolla* and *Cliopsis* spp. are an order of magnitude lower than those of the more active *Clione limacina* and *Limacina helicina* (Biggs D.C., 1977; Seibel B.A. et al., 2007).

As mentioned earlier, pteropod food preferences are among other things size-dependent (chapter 2.2.4). Perissinotto R. (1992) suggested pteropods might not always fully benefit from phytoplankton blooms in case they cannot effectively graze on phytoplankton due to unfavourable phytoplankton size structure and consequential inability of pteropods to ingest the cells of the phytoplankton species contributing to the blooming event. Two studies conducted in the Southern Ocean during spring supported this argument. Lower daily ingestion rates of *Limacina* spp. were recorded by Perissinotto R. (1992), when during the time of survey 86 % of total phytoplankton stock was composed of 2-20 µm and <20 µm particles (nano- and microplankton respectively), whereas *Limacina* spp. preferentially grazed on <5 µm particles. The higher daily ingestion rates for *Limacina* spp. were recorded by Bernard K.S. (2006), when the phytoplankton biomass was almost entirely dominated by pico- (<2 µm) and nano-plankton, preferential food particles of *Limacina* spp.. It is important to point out the variability in ingestion rates between the studies could also be due to varying food concentration. However, much higher general chl-a concentration was recorded by Perissinotto R. (1992), implying that food composition, not only food abundance, affected pteropod abundances in both studies. A similar effect of food quantity and quality on the population observed for the case of *Limacina helicina* can also be traced higher up on the food chain. In years of limited primary productivity, or less nutritious food sources, *Limacina* possibly reduced lipid stores and thus decreased caloric values for its primary predator *Clione limacina* and other predators (Maas A.E. et al., 2011).

2.3.2 Predation

DVM is a known behaviour of visual predator avoidance among zooplankton organisms (Bollens S. et al., 1992; Lampert W., 1989; Williamson C.E., 2011). Zooplankton grazes in the food-rich surface layers at night and then descends and remains at greater depths during the day to minimize its exposure to visual predators (Lampert W., 1989; Hays G.C. et al., 2001; Fortier M. et al., 2001). DVM is also a behaviour observed for many pteropod species (Wormuth R.H., 1981; Hunt B.P.V. et al., 2008). In the Arctic Ripfjorden (Svalbard, 80° N), distinct DVM patterns were observed among adult and juvenile stages of *Limacina helicina* during autumn period (when there was a significant difference in light conditions between day and night) (Falk-Petersen S. et al., 2008). *Limacina helicina* represented an important prey of polar cod in that area, which migrated into the surface layers during the day to feed on pteropods (Falk-Petersen S. et al., 2008). Responding with predator avoidance behaviour, the adult *Limacina helicina* migrated daily, moving from deep water (150 m) during the day, to the surface (10-75 m) during the night (Falk-Petersen S. et al., 2008). Even the veliger and juvenile stages of *Limacina helicina* showed a distinct change in the vertical distribution, appearing in highest numbers (up to 8000 ind. m^{-3}) at 0-20 m during night and at 20-50 m during the day, showing the ability of migrating according to their needs (Falk-Petersen S. et al., 2008).

Visual predation at certain depth can be reduced due to higher water turbidity; a higher turbidity in meso- and eutrophic sites could have been one of the reasons why the DVM patterns recorded by Andersen V. et al. (1997) in NE tropical Atlantic for *Clio pyramidata* and other pteropod species in these two environments exhibited lower DVM amplitudes, whereas in less turbid oligothropic site, the DVM amplitude of pteropods was higher. As the eutrophic

sites are very rich with nutrients, certain marine organisms were concentrated both day and night in rich phytoplankton upper layers, because the loss due to predation was compensated by the plentiful food (Andersen V. et al., 1997).

Some species of gymnosomes produce fish anti-feedant chemicals as a defence to fish predation (Bryan P.J. et al., 1995; Phelger C.F. et al., 1999). *Clione antarctica* produces pteroenone linear b-hydroxyketone (C14H2402) (Bryan P.J. et al., 1995) and *Spongiobranchaea australis* a polyunsaturated fatty acid (14:3) (Phelger C.F. et al., 1999). Bryan P.J. et al. (1995) confirmed Antarctic fish, which feed on planktonic organisms, do not prey on *Clione antarctica* even though its dense populations offer a rich source of potential nutrients and energy. It is possible that due to the reduction in predation pressure imparted by the anti-feedants, the vertical distribution of these gymnosomes may be more strongly determined by their prey rather than predator avoidance behaviour (Hunt B.P.V. et al., 2008). These species may consequently have limited importance for higher trophic levels (Bryan P.J. et al., 1995).

2.4 Adaptations and responses of pteropods to the abiotic factors in the environment

Based on the results of the experimental and observation studies from the literature, a detailed review is drawn out to provide valuable insight of pteropod interactions with their physical environment. Pteropod responses and adaptations to different abiotic factors (temperature, salinity, pressure, oxygen levels), including species specific responses and responses to often synergetic effects of abiotic and biotic (primarily food abundance) factors are reviewed.

2.4.1 Metabolic rates

A combination of biotic and abiotic factors can affect metabolic rates of pteropods. Metabolic rates depend on ambient temperature (Comeau S. et al., 2010a; Maas A.E. et al., 2012b), oxygen concentration (Maas A.E. et al., 2012b), individual body mass (Smith K.L. Jr. and Teal J.M., 1973; Seibel B.A. et al., 2007; Maas A.E. et al. 2011, 2012a, 2012b), lifestyle (Seibel B.A. et al., 2007), pressure (Smith K.L. Jr. and Teal J.M., 1973), regional primary productivity and feeding history (Seibel B.A. and Dierssen H.M., 2003; Seibel B.A. et al., 2007; Maas A.E. et al., 2011; Seibel B.A. et al., 2012; chapter 2.3.1).

The oxygen consumption rate in aerobic organisms is an indicator of organism general metabolic activity (i.e. all physical and chemical processes in a living organism), as the aerobic organisms form the energy (ATP) for powering most of their metabolism (cellular activity) through aerobic cellular respiration in mitochondria by oxidizing organic compounds (Abercrombie M. et al., 1992). Therefore, oxygen consumption rate is measured in experimental studies to determine metabolic rates of organisms (de Weir J.B.V., 1949), also in case of pteropods (Seibel B.A. et al., 2007; Maas A.E. 2011, 2012b; etc.).

Changing temperature and oxygen concentration are thus considered important abiotic factors affecting metabolic rates of marine zooplankton, including pteropods (Christou E.D. et al. and Moraitou-Apostolopoulou M., 1995; Comeau S. et al., 2010a; Seibel B.A., 2011; Maas A.E. et al., 2012b), as the successful and sufficient oxygen uptake is correlated to the ambient temperature and oxygen concentrations as well as the specific needs of the organism (Pörtner H.-O., 2001). Stable metabolic rates are usually encountered only in some parts of the temperature range that zooplankton inhabits (Christou E.D. and Moraitou-Apostolopoulou M., 1995). However, the range of temperatures at which the organisms are still able to maintain a sufficient import of oxygen supply without experiencing stress, is their

thermal niche (Pörtner H.-O., 2001). Migrators are generally adapted to experience greater temperature and oxygen changes than non–migrators (Wormuth J.H., 1981; Seibel B.A., 2011) and are thus expected to have a broader thermal window and higher tolerance of hypoxia than non-migrators (Seibel B.A., 2011; Maas A.E. et al., 2012b; Storey K.B. and Tanino K.K., 2012).

The respiration rates generally increase with higher temperature, due to the increased energy demands of organisms in warming environment (Pörtner H.-O. 2001, 2008; Maas A.E. et al., 2012b; Seibel B.A. et al., 2007). Smith K.L. Jr. and Tiel J.M. (1973) recorded increased respiration rates in correlation with increasing temperature for thecosomatous pteropods *Diacria trispinosa, Cuvierina columnella, Clio pyramidata* and *Limacina helicoides*. Elevated respiration rates of *Limacina helicina* were also recorded at elevated (4°C in comparison to control 0°C) temperature in the study of Comeau S. et al. (2010a). Similarly, Seibel B.A. et al. (2007) recorded oxygen consumption rates of both, gymnosomes (*Clione antarctica, Clione limacina, Pneumodermopsis* spp., *Thliptodon* spp., *Cliopsis krohni, Notobranchia grandis*) and thecosomes (*Clione limacina, Cavolinia tridentata, Corolla* spp.) to increase with higher temperatures.

General response of pteropods to lower temperatures and oxygen concentrations is to slow down their metabolic rates and consequently, lower their energy needs (Comeau S. et al., 2010a; Mass et al., 2012b). Suppression of metabolic rates is a strategy for extending survival time during exposures to short-term stressful conditions, such as food deprivation, hypoxia, hypercapnia or co-occurrence of these environmental stressors (Guppy M. and Withers P., 1999; Seibel B.A. et al., 2012; Maas A.E. et al., 2012b). Certain pteropod species (*Diacria quadridentata, Cavolinia inflexa, Creseis virgula, Cavolinia logirostris, Clio pyramidata* and *Hyalocylix striata)* in the Eastern Tropical North Pacific (ETP) were observed to be able to reduce metabolic rates by 60-75% when exposed to experimental temperatures 11-20°C, representing the temperature range of the upper 200 m of the water column i.e. their approximate diel migration range (Maas A.E. et al., 2012b). In low oxygen environment (~30 µmol O_2 kg^{-1}), three species of pteropods (*Hyalocilix striata, Cavolinia longirostris* and *Creseis virgula*) showed an additional 35-50% decrease in oxygen consumption at low temperatures (11°C) (Maas A.E. et al., 2012b). Combined, low temperature and hypoxia thus suppressed the metabolic rates of certain pteropods by ~80-90% - an ability helping these pteropods to survive short-term hypoxic conditions when migrating into deeper oxygen depleted layers as with lower metabolism they reduce their demand for oxygen (Maas A.E. et al., 2012b). The extent of metabolic suppression is species-specific and likely dependent on physiological adaptation to hypoxia and the thermal niche of the species (Pörtner H.-O. 2001, 2008; Maas A.E. et al., 2012b). Metabolic suppression is typically achieved by shutting down expensive physiological processes, such as protein synthesis (reducing growth and reproduction) and ion transport, thus lowering the energy needs (Guppy M. and Withers P., 1999). However, as the two biological functions impacted by stress conditions are growth and reproduction, a long-term metabolic suppression resulting from chronic exposure to stressful environment might have deleterious consequences for the whole population (Seibel B.A. et al., 2012).

In experiments, respiration rates of pteropods generally increased with increased pressure and temperature, although the effect was species-specific (Smith K.L. Jr. and Tiel J.M., 1973). Respiration rates of the three epipelagic species, *Diacria trispinosa, Cuvierina columnella* and *Clio pyramidata* were responsive to changing temperature and pressure: decreasing temperature alone caused a decrease in respiration rates while pteropods were descending inside the limits of their normal distribution range, whereas the combined effect of temperature and pressure caused a significant increase in respiration rates at greater depths, outside of their normal migration range (Smith K.L. Jr. and Teal J.M., 1973). Bathypelagic species *Limacina helicoides,* adapted to deep water dwelling, was more strongly influenced by temperature in shallower depths outside its depth range and less

inside their depth range. Pressure, on the other hand, had no significant effect on the respiration rates of *Limacina helicoides*, except at extreme depths (above 150 atm). These responses show pteropods were adapted to maintain a fairly constant metabolism through their natural vertical range (Smith K.L. Jr. and Teal J.M., 1973).

The oxygen consumption rates also decline with higher wet body mass (Smith K.L. Jr. and Teal J.M., 1973; Seibel B.A. et al., 2007; Maas A.E. 2012a, 2012b). Maas A.E. et al. (2012a, 2012b) recorded a relationship between oxygen consumption and body mass of five species of thecosome pteropods from the Pacific Ocean and the oxygen consumption declined with higher body mass.

Metabolic rates of animas also change with their activity (Ikeda T., 1989). A close relationship between locomotory capacity and the metabolic rates of gymnosomes and their thecosomatous prey was observed (Seibel B.A. et al., 2007; chapter 2.3.1). Life at lower temperatures resulted in limited energy available for locomotion (swimming velocity) due to depressed mitochondrial ATP production (Seibel B.A. et al., 2007). Therefore, a compensation mechanism for locomotory capacity in cold waters led to elevated metabolic rates in polar species, like in the active gymnosome predator *Clione antarctica* (Seibel B.A. et al., 2007). In other words, some cold-water predators such as *Clione antarctica* evolved high metabolic capacity in order to play its thropic role as an active predators under high energetic demands due to the extreme environmental conditions (Seibel B.A. et al., 2007). In comparison with these selection driving mechanisms, temperature and the body size of organisms can be relatively minor determinants of metabolic rates (Seibel B.A. et al. (2007).

In addition, as described in chapter 2.3.1, low food abundance or starvation can also result in substantial suppression of metabolic rates, such as 20% decrease in metabolic rate of *Limacina helicina antarctica* (Seibel and Dierssen, 2003; Maas A.E. et al., 2011) and a 30-50% decrease in metabolic rates of their predators, *Clione limacina* and *Clione antarctica* (Seibel B.A. et al., 2007; Maas A.E. et al., 2011).

2.4.2 Growth and calcification rates

The growth of pteropods is associated with shell growth measured as calcification rate (Fabry V.J., 1989; Schalk P.H., 1990; Comeau S. et al. 2009, 2010a; Lischka S. et al., 2011). The calcification rates of *Limacina helicina* were recorded to decrease with decreasing aragonite saturation (Comeau S. et al., 2010a; chapter 2.2.3). As the $CaCO_3$ saturation state is temperature, pH and salinity dependant, higher saturation in warmer water promotes calcification and conversely, acidification (lower pH) negatively affects calcification abilities (Fabry V.J. et al., 2008; Comeau S. et al. 2009, 2010a, 2010b; Lischka S. et al., 2011; chapter 2.6.2). However, the understanding, which abiotic factors and their mechanism of action impact the (shell) growth of pteropods is vague and remains to be disclosed. The growth rates have not yet been documented for many pteropods species and the currently existent data is difficult to compare due to different experimental methods and units used. Below is the summary of currently available data on calcification rates.

As the growth rate is correlated with metabolic rate, it is thus dependend on temperature, oxygen concentration, food abundance and other factors affecting metabolic rates (chapter 2.4.1). Comeau S. et al. (2010a) recorded increased calcification rates of *Limacina helicina* at elevated temperatures, whereas Lischka S. et al. (2011) showed that there was no correlation. In other marine calcifying organisms, such as foraminifers, bivalves and corals, the calcification rates were observed to increase with increasing aragonite saturation (Lea D.W. et al., 1995; Silverman J. et al., 2007) or/and temperature although the temperature had a negative impact on $CaCO_3$ uptake when exceeding the optimal temperature range (Silverman J. et al., 2007). The abiotic conditions for optimal calcification rates are

considered species-specific (Silverman J. et al., 2007). Simultaneous effects of abiotic factors such as temperature and aragonite saturation on calcification are difficult to interpret (Silverman J. et al., 2007).

Fabry V.J. (1989) estimated the growth rate as the rate of Ca^{2+} deposition in the shell for *Clio pyramidata* to be 1.8 mg $CaCO_3$ m^{-2} day^{-1} and for *Limacina helicina* to be 2.6 mg $CaCO_3$ m^{-2} day^{-1} (at 10.7°C, calculated with instantaneous growth method; Fabry V.J., 1989). Bednaršek N. et al. (2012a) also studied the growth rates of *Limacina helicina* in the Southern Ocean, measuring shell length growth over time. The average interannual growth rate was 0.01 mm day^{-1} (Bednaršek N. et al., 2012a). According to Bednaršek N. et al. (2012a), the growth did not stop during the winter period – the autumn/winter rate was similar as the summer rate, although it is unclear how *Limacina helicina* managed to maintain such growth over winter in spite of low productivity levels (Bednaršek N. et al., 2012a). Higher interannual growth rate relative to individual shell diameter was observed in younger (1-6 month old) and smaller specimen in comparison with older (1-1.5 years old) specimen of *Limacina helicina* - 0.44% day^{-1} compared to 0.24% day^{-1}, respectively (Bednaršek N. et al., 2012a). Internannual growth measurements were also performed by Wells F.E. (1976) on four euthecosome pteropod species in the North Atlantic (Caribbean Sea, Barbados), with the growth rate ranging between 0.01 mm day^{-1} (*Creseis virgula)*, 0.005 mm day^{-1} (*Limacina bulimoides)*, 0.004 mm day^{-1} (*Limacina inflata)* and 0.0033 mm day^{-1} (*Limacina trochiformis).*

During their earliest life stages as eggs, pteropods form a protoconch (embryonic shell), whereas the adult shell is formed soon after hatching (Van der Spoel S., 1967). As the pteropod eggs occur near the surface, the protoconch is formed under environmental conditions of the sea surface water layers (Schalk P.H., 1990). Mean protochonch volumes of the pteropod population were observed significantly related to sea surface temperatures, with smaller volumes at higher temperatures (Schalk P.H., 1990). Furthermore, the size of the specimen belonging to certain pteropod species may be correlated with distribution patterns, directly dependent on temperature and the ability of pteropods to adapt to different environmental circumstances (Schalk P.H., 1990). A decrease of average adult size with seasonally increasing temperature was observed for species with wide distribution range in Indo Pacific Ocean: *Diacria costata, Diacria rampali, Cavolinia longirostris longirostris, Clio pyramidata* and *Cavolinia longirostris strangulata* (Schalk P.H., 1990). As the temperature decreased due to the seasonal upwelling of cold nutrient rich waters, higher food abundance as a one of the important factors contributing to increased size of the specimen was also considered (Schalk P.H., 1990). Furthermore, size variation across different latitudes was observed by Van der Spoel (1970) for *Cavolinia longirostris angulosa and Cavolinia longirostris longirostris*, which exhibited smaller specimen in warmer equatorial waters compared to higher tropical latitudes. Furthermore, *Clione limacina* appeared in greater sizes in cold-water high-latitudinal areas (Arctic), whereas in temperate waters of subarctic, North Atlantic, North Pacific, smaller sized specimen were observed (Lebour M.V., 1931 cited in Böer M. et al., 2005). Conversely, Lischka S. et al. (2011) recorded no significant influence of temperature effecting the shell growth and calcification of juvenile *Limacina helicina* specimen, although this might have been due to the experimental constraints. Several studies confirmed that metabolic rates declined at lower temperatures (Smith K.L. Jr. and Tiel J.M., 1973; Seibel B.A. et al., 2007; Comeau S. et al., 2010a; Maas A.E. et al., 2012b; chapter 2.4.1), where suppression of metabolism helped organisms to conserve energy in stressful conditions, at the expense of more energy demanding processes, such as growth and reproduction (Guppy M. and Withers P., 1999).

2.4.3 Reproduction

The reproduction of pteropods is seasonal, dependent upon favourable environmental conditions (Lalli C.M. and Gilmer R.W., 1989; Dadon J.R. and de Cidre L.L., 1992). In

stressful environment, such as during the times of low food availability, pteropods tend not to spend the energy for energetically costly processes, such as on reproduction and development, but on maintaining basic life functions (Böer M. et al. 2005, 2007; Seibel B.A. et al., 2007). Polar regions (the Arctic Sea and the Southern Ocean) are environments with extreme environmental conditions and pronounced seasonality in light conditions, temperature and ice cover, resulting in short and intensive blooms of primary producers (Sakshaug E., 2003). In the major part of the Southern Ocean, the primary production is very limited, due to low temperatures, very low light availability through the year and constant high winds, which reduce water column stability and generate deep mixed layer (Laubscher R.K. et al., 1993; Balarin M.G., 1999; Froneman P.W. et al., 2001). As a result, pteropods mainly reproduce in spring, summer or autumn, to take the advantage of seasonally higher food abundance in these periods (Kobayashi H.A., 1974; Lalli C.M. and Gilmer R.W., 1989; Böer M. et al., 2005; Gannefors C. et al., 2005; Bernard K.S., 2006; Bednaršek N. et al., 2012a). Thus, the reproduction of thecosomatous pteropods is correlated with abundant primary production driven by abiotic factors of favourable light, temperature (annual heating of surface waters) and water mixing (Mileikovsky S.A., 1970; Böer M. et al., 2007; Gannefors C. et al., 2005). Consequently, the reproduction rates of Gymnosomes can be indirectly impacted by the phytoplankton scarcity due to growth limiting environmental conditions as well, because they depend on thecosomes as their predominant prey (Lalli C.M. and Gilmer R.W., 1989; Seibel B.A. et al., 2007; Hunt B.P.V. et al., 2008; Seibel B.A. and Dierssen H.M., 2003).

The environmental factors may also initiate or delay the maturation process of organisms (Byrne M., 2011; Dadon J.R. and de Cidre L.L., 1992). A geographic factor affecting maturation process was observed for *Limacina retroversa* in the Argentine Sea, where the difference in hydrology dynamics as a result of a quick turnover rate of water in slope waters between the shelf and slope area caused pteropods in the slope waters to mature faster (Dadon J.R. and de Cidre L.L., 1992).

2.4.4 Ingestion rate

The correlation of ingestion rates and temperatures for pteropods has not been examined specifically, but the correlation of ingestion rates with chl-a concentration and food quality (size of phytoplankton cells) is usually considered. There is not a lot of data on ingestion rates of different pteropod species available in the literature. Ingestion rate was generally calculated as a product of ingested pigment (gut pigement destruction) and gut evacuation rate. The calculation procedure can be seen in Annex B, where also the primary production rates in C m^{-2} day^{-1} units are presented.

The majority of studies on ingestion rates have calculated the daily ingestion rate for *Limacina* spp.*,* but none of these studies focused on the correlation or the effect of temperature on ingestion rates. Ingestion rates calculated for *Limacina helicina* spp*.* in the Nortern Atlantic at the temperature between 9°-10°C were ranging between 7-32 µg (pigm.) m^{-3} day^{-1} (Perissinotto R., 1992), the values transformed for the coherency of units purposes into 31-302 (161±110) ng (pigm.) $ind.^{-1}$ day^{-1} (Hunt B.P.V. et al., 2008). This study also found out that gut pigment levels for *Limacina* spp. (and other zooplankton groups) were always higher at night, pointing towards the influence of diurnal feeding cycles on gut pigment content and consequently ingestion rates (Perissinotto R., 1992). In the Southern Ocean at the (ambient temperature of experiments performed on the deck) of approximately -1°C (NODC-WOD, 2012), ingestion rates of *Limacina* spp. were one order of magnitude higher (2103 ng (pigm.) $ind.^{-1}$ day^{-1}), suggested to be such due to higher average individual dry masses of pteropods (Pakhomov E.A. and Froneman P.W., 2004). The same study also recorded extremely high ingestion rates among pteropods displayed by *Clio pyramidata sulcata*, equivalent to 16627-27757 ng (pigm.) $ind.^{-1}$ day^{-1}, during times of chl-a biomass

ranging from 20-54 mg (pigm) m^{-2} (Pakhomov E.A. and Froneman P.W., 2004). Average ingestion rates of *Limacina retroversa* recorded in the Southern Ocean were 4146.51 ng (pigm.) $ind.^{-1}$ day^{-1} (std= 1296.82), 4128.68 ng (pigm.) $ind.^{-1}$ day^{-1} (std= 892.23), 4196.88 ng (pigm.) $ind.^{-1}$ day-1 (std= 8.56) at average temperatures 4.94°C, 5.79°C and 4.28°C, respectively and chl-a concentrations of 15.1-28.3 mg m^{-2}, 10.8-12.4 mg m^{-2} and 7.2-8.7 mg m^{-2}, respectively. Furthermore, Pakhomov E.A. and Perissinotto R. (1997) recorded ingestion rates of *Limacina helicina* in the Subtropical Convergence (the boundary of Southern Ocean) were 540.5 ng (pigm.) $ind.^{-1}$ day^{-1}, 701.6 ng (pigm.) $ind.^{-1}$ day^{-1} and 170 ng (pigm.) $ind.^{-1}$ day^{-1}, with primary production of 34.3 mg chl-a m^{-2}, 45.9 mg chl-a m^{-2} and 32.3 mg chl-a m^{-2}, respectively and at water temperature of 11°-12°C. Ingestion rate of *Limacina helicina* estimated from the measurements of a 5 day incubation experiment at 0°C and chlorophyll-a concentration of 5.65 µg L^{-1}, was 13.1 µg C $ind.^{-1}$ h^{-1} (Elliot T.D. et al., 2008).

2.4.5 Diel and seasonal vertical distribution and migrations in the water column

Vertical (diurnal and seasonal) distributions of pteropods were observed to be influenced and limited by various abiotic factors, such as light intensity (turbidity) (Andersen V. et al., 1997), temperature (Chen C. and Bé A.W.H., 1964; Lischka S. et al., 2011), water turbulences (Mackas D.L. and Galbraith M.D., 2002; Tsurumi M. et al., 2005) and oxygen depletion zones (Maas et al., 2012b). Biotic environmental factors, such as food availability and predator-avoidance (Mileikovsky S.A., 1970; Almogi-Labin A. et al., 1988; Benfield M.C. et al., 1996; Falk-Petersen S. et al., 2008) influence vertical distribution and DVMs of pteropods in synergy with abiotic factors.

DVMs of zooplankton can be initiated by various cues, with the most important factor being the changes in the light intensity, and thus food availability and visibility (Forward R.B., 1988; Andersen V. et al., 1997; Cottier F.R. et al., 2006). Andersen V. et al. (1997) observed decreasing mean DVM amplitude of *Clio pyramidata* from oligotrophic (475 m), through mesotrophic (305 m) and to eutrophic (70 m) sites. The euphotic zone of oligotrophic site was much deeper (105 m) than the zone in mesotrophic (27 m) and eutrophic site (20-25 m), due to the high chlorophyll concentration in the upper 30 m of the latter two sites (Morel A. et al., 1996). Consequently, pteropods in mesotophic and eutrophic areas migrated to shallower daytime depths (Andersen V. et al., 1997). Other species, *Cuvierina columnella* and *Styliola subula* also performed DVMs in oligotrophic site, migrating 290 m and 365 m, respectively (Andersen V. et al., 1997). Beside the light conditions, the three different trophic sites differed strongly in phytoplankton abundance, high in eutrophic and always low in oligotrophic site, whereas the climatic conditions were similar at all three sites throughout the whole year (Andersen V. et al., 1997).

Seasonal vertical migration was proposed to be an overwintering strategy for pteropods, where moving into deeper and colder water layers slows down their metabolism and the life costs to survive low food abundance during winter (Lischka S. et al., 2011). Chen C. and Bé A.W.H. (1964) observed the depth distributions of certain thecosomatous pteropods that were influenced by the seasonal changes in the temperature stratification of the water column. *Limacina inflata* and *Styliola subula* were proposed to daily migrate within their optimal temperature range, which upon observation was in deeper and colder water layers during winter/spring season and in warmer surface waters during the summer/autumn season (Chen C. and Bé A.W.H., 1964). The optimum temperature ranges of these pteropods during different seasons coincided with optimum calcification depths (Juranek L.W. et al., 2003). It was suggested, vertical distribution of pteropods is restricted to aragonite saturated water masses (Gangstø R. et al., 2008). However, pteropods were also observed to spend a significant amount of time outside of their optimal temperature ranges (Chen C. and Bé A.W.H., 1964; Juranek L.W. et al., 2003) as well as found in the waters

undersaturated with respect to aragonite (Bednaršek N. et al., 2012b). Moreover, factors influencing pteropod seasonal and diel vertical migration were also the depth of chlorophyll maximum and predator abundance and distribution (Almogi-Labin A. et al., 1988; Juranek L.W. et al., 2003).

Vertical distribution of pteropods, such as of *Diacria quadridentata, Cavolinia uncinata* and *Cavolinia inflexa* in the ETP, can be limited by the oxygen depleted zones with low pH (also occurring at depth in times of high productivity in the surface waters), representing stressful environment (Maas A.E. et al. 2012a, 2012b). On the other hand, some pteropod species including *Hyalocylix striata*, *Clio pyramidata*, *Cavolinia logirostirs* and *Creseis virgula* in ETP were observed to daily migrate into hypoxic zones, thus displaying the ability to successfully survive short-term hypoxia, although not completely without cost as they decreased their metabolic rate during the time of experiencing hypoxia (Maas A.E. et al., 2012b).

Another factor limiting DVM of diel migrators such as *Clio pyramidata* and *Limacina helicina* were strong winds and turbulences, in times of which pteropods abstained from or greatly restricted their nocturnal upward migration (Mackas D.L. and Galbraith M.D., 2002; Tsurumi M. et al., 2005). Tsurumi M. et al. (2005) suggested these thecosomatous pteropods sank deeper into calmer water because strong turbulence disrupted their ability to feed with deployed mucous webs.

2.4.6 Geographic distribution

The geographical ranges of marine organisms depend on the level of their mobility, i.e. mode of life and their tolerance ranges for physical factors (such as salinity, pressure, stratification, oxygen concentration, pH and temperature) along with the biotic factors (such as food abundance, competition and predation), additionally shaping the biogeography of species (Pörtner H.-O. 2002, 2008). Important abiotic environmental factors influencing geographic distribution of pteropods are water currents (Redfield A.C., 1939) and seasonal hydrographic changes such as monsoons (Schalk P.H., 1990) and eddies (Mackas D.L. and Galbraith M.D., 2002), under influence of which pteropods are often carried to regions far away from their original habitat. In there, their survival and the persistence of their populations are not guaranteed, as they might not find environmental conditions favourable (Redfield A.C., 1939). On the other hand, if the conditions in the new environments are more favourable than in their original environment, pteropods can occur in high abundances (Mackas D.L. and Galbraith M.D., 2002).

The geographical distribution range of ectothermic marine animals is limited by the temperature range within the natural habitat to which they are acclimated to, as the successful functioning of their organism is limited by the insufficient oxygen supply in comparison with oxygen demand outside of their thermal niche (Pörtner H.-O. 2001, 2002, 2010). Ectothermic animals are capable to survive at temperatures higher or lower from their thermal range only for a limited amount of time, because their feeding and growth success under thermal and oxidative stress decrease and therefore their long-term fitness reduces progressively (Pörtner H.-O., 2010). They have species-specific geographic distributions and are physically adapted to tolerate specific temperature regime in their natural environment (Pörtner H.-O. 2001, 2002), i.e. pteropods naturally experience the narrow range of constant low temperatures in high-latitudes (Pörtner H.-O., 2002; Seibel B.A. et al., 2007; Rosenthal J.J.C., 2008) or greater temperatures fluctuations in warmer temperate regions (Juranek L.W. et al., 2003).

Furthermore, currents present a paramount physical factor influencing geographical distribution of pelagic organisms, such as pteropods, which can be carried by the currents from their original area to seasonally or locally appear in specific foreign regions (Redfield

A.C., 1939). Such is the case of naturally sub-Antarctic species *Limacina retroversa,* which was recorded south of Antarctic Polar Front, due to mixing of water masses as a result of eddy formation in the Southern Ocean (Bernard K.S. and Froneman P.W., 2009). Similarly, the occurrence of *Limacina retroversa* in the Gulf of Maine, but originating from Scotian Shelf, was due to the cyclonic eddy (Redfield A.C., 1939). However, as a result of unsuccessful reproduction and continuous cyclonic drift about and out of the Gulf, *Limacina retroversa* in the Gulf of Main was observed to be unable to sustain a stable, permanent population (Redfield A.C., 1939; Ashjian C.J. et al., 2001). Nevertheless, these occasional immigrations made pteropods an important part of the local marine ecosystems for certain amounts of time (Redfield A.C., 1939). Subarctic species *Limacina helicina* (endemic for North Pacific subarctic Gyres) and subtropical *Clio pyramidata* (endemic for lower latitude regions, but carried northward by the winter currents), which appear abundant over British Columbia continental slope, were both transported long distances seaward from coastal/continental margin environments into subarctic North Pacific (the Alaska Gyre) by large anticyclone Haida eddies formed annually along the eastern margin of the Alaska Gyre (Mackas D.L. and Galbraith M.D., 2002). The abundances within eddies often surpassed the concentrations of the areas of their origin (including both, the region of endemic population and the region of the population being the source for the eddy population, which is not necessarily the endemic region at the same time) as both species were very successful in colonizing the eddies (Mackas D.L. and Galbraith M.D., 2002).

Moreover, seasonal hydrographic changes, such as monsoons and related changes in the environment, differently affect the abundance and distribution patterns of pteropods, depending on their living environment preferences (Schalk P.H., 1990). In the Indo-Pacific Banda and Arafa Seas, SE monsoon causes upwelling of nutrient rich cold water (from June-September) with subsequent high primary production; NW monsoon causes downwelling, stratification, depletion of nutrients and low primary production (from December-March) (Schalk P.H., 1990). The effects of these two monsoons on pteropods varied depending on the pteropod species (Schalk P.H., 1990). *Diacria costata* was among the species exhibiting wide distribution during both monsoon seasons, with higher abudnaces during SE monsoon period (Schalk P.H., 1990). On the other hand, *Cavolinia longirostris longirostris* appeared in low abundaces in oligothropic downwelling conditions – during NE monsoon it was only found in the areas where the effects of downwelling were less distinct, but it spread around the entire area during SE monsoon upwelling period (Schalk P.H., 1990). Finally, *Cavolinia globulosa, Diacria danae, Cavolinia uncinata uncinata pusilla* and other species exhibited broader distribution and higher abundances during NW monsoon season, clearly indicating a preference for the oligothropic environment (Schalk P.H., 1990).

2.5 Role of pteropods in the marine environment

2.5.1 Ecological role

Pteropods represent an important part of marine food webs and can significantly contribute to biomass of a certain size-class of zooplankton (e.g. meso-/macro-zooplankton), especially in polar regions when reaching high biomass concentrations (Boysen-Ennen E. et al., 1991; Pane L. et al., 2004; Bernard K.S., 2006; Hunt B.P.V. et al., 2008). They can reach densities of thousands of individuals per m^{-3} in some regions and also contribute substantially towards the total zooplankton densities (Hopkins T.L., 1987; Ward et al. P., 2003; Pakhomov E.A. and Froneman P.W., 2004; Pane L. et al., 2004; Hunt et al., 2008). The contribution to zooplankton biomass can considerably vary regionally, seasonally and between years (Pane L. et al., 2004; Seibel B.A. and Dierssen H.M., 2003; Bernard K.S., 2006).

2.5.1.1 Grazing impact

The correlation between phytoplankton blooms and pteropod abundance has been observed in several studies (Almogi-Labin A. et al., 1988; Seibel B.A. and Dierssen H.M., 2003; Bernard K.S., 2006). The grazing impact of pteropods on phytoplankton stock may be substantial due to their high ingestion rates, such as observed in case of *Clio pyramidata* and *Limacina helicina* (Pakhomov E.A. and Froneman P.W., 2004; Hunt B.P.V. et al., 2008; Bernard K.S. and Froneman P.W., 2009; Elliot D.T. et al., 2008). *Limacina retroversa* was at certain times observed to contribute substantially to total mesozooplankton numbers and was considered a major grazer in the zooplankton community of Polar Frontal Zone ecosystem in the Indian sector of the Southern ocean (Bernard K.S., 2006). The grazing contribution of *Clio sulcata* and *Limacina helicina* recorded in the Southern Ocean (Spring Ice Edge Region) during austral summer amounted to 52.5 % of the total grazing impact in the region (Pakhomov E.A. and Froneman P.W., 2004). Similar level of grazing impact was reported in the Polar Frontal Zone (Southern Ocean), where *Limacina retroversa* contributed an average of 54.3% to 59.5% of the total grazing impact, while representing approximately 8% to 12% of total zooplankton abundance, respectively (Bernard K.S., 2006). Elliot D.T. et al. (2008) estimated the grazing impact of *Limacina helicina* in the Ross Sea (Antarctica), feeding on under ice blooms of haptophyt *Phaeocystis antarctica* to be 10-50% of primary production per day. The estimates for *Limacina helicina* spring grazing impact in the Prince Edward Archipelago austral autumn were comparably lower, accounting to 2.6-19% of the primary production per day (Perissinotto R., 1992), possibly due to lower pteropod abundances. Thecosomatous pteropods, such as *Limacina* spp., are the link between primary production and higher trophic levels, assisting in the transfer of carbon from short lived organic carbon pool to long-lived organic carbon pool (Legendre L. and le Fèvre J., 1992). However, Perissinotto R. (1992) also suggested, that pteropods might not always fully benefit from a phytoplankton blooms in case where they cannot effectively graze on phytoplankton due to unfavourable phytoplankton size structure (chapter 2.3.1). Since the pteropod abundances vary seasonally this is expected to be reflected in the grazing impact of pteropods, likely coinciding with the peak in reproductive output (Bernard K.S., 2006).

2.5.1.2 Food source for other organisms

Thecosomes are the most important food source of gymnosomes (Connover R.J. and Lalli C.M., 1972; Seibel B.A. and Dierssen H.M., 2003; Böer M. et al., 2005), with the prey-predator relationship correlated in size (Lalli C.M. and Gilmer R.W., 1989), distribution and abundance (Connover R.J. and Lalli C.M., 1972; Seibel B.A. and Dierssen H.M., 2003; Böer M. et al., 2005). Pteropods also represent an important food source for other marine organisms of the higher thropic levels, such as pelagic and demersal fish such as cod, salmon, herring and others (Lalli C.M. and Gilmer R.W., 1989; Armstrong J.L. et al., 2005; Hunt B.P.V. et al., 2008), carnivorous zooplankton such as chaetognaths, heteropods, ctenophores, medusa, siphonophores (Lalli C.M., 1970; Lalli C.M. and Gilmer R.W., 1989, Pakhomov E.A. and Perissinotto R., 1996, Froneman E.A. and Pakhomov P.W., 1998; Böer et al., 2005), amphipods (Pakhomov E.A. and Perissinotto R., 1996; Bernard K.S., 2006), cephalopods, seabirds (Hunt B.P.V. et al., 2008) and marine mammals such as whales (Lalli C.M. and Gilmer R.W., 1989).

2.5.2 Biogeochemical role

Biogeochemical role of pteropods is realised through their contribution to vertical flux of organic and inorganic carbon i.e. the biological pump channelling carbon from the surface

into the ocean interior (Almogi-Labin A. et al., 1988; Collier R. et al., 2000, Francois R. et al., 2002; Hood R.R. et al., 2006).

2.5.2.1 Organic Carbon export

Pteropods are involved in organic carbon export out of the surface waters through numerous pathways. One way of contribution to carbon flux is through formation of aggregates out of mucous webs used for feeding, together with the small particulate organic material trapped in them (Bathmann U.V., 1991; Noji T.T. et al., 1997). The webs can be lost due to disturbance during feeding, such as increased surface turbulence (Tsurumi M. et al., 2005) or predator disturbance (Gilmer R.W. and Harbison G.R., 1986). Mucous is also partly excreted as pseudo-faeces when the undesirable material/food particles get rejected (Gilmer R.W. and Harbison G.R. 1986, 1991; Gilmer R.W., 1990).

Additional contribution to vertical organic carbon flux is through excretion of faecal pellets in the form of solid waste products (Noji T.T. et al., 1997). Faecal pellets of zooplankton can be a major component of the vertical transport of organic matter to the deep ocean due to fast sinking rates (Komar P.D. et al., 1981; Bruland K.W. and Silver M.W., 1981). The result of intensive pteropod feeding can therefore be a massive vertical flux of organic matter out of the surface layer (Bathmann U.V. et al., 1991).

In the Southern Ocean, *Limacina helicina* significantly contributed to the transport of organic carbon to the deep ocean due to the robustness (resistance to mechanical and microbial degradation) and fast sinking rates of its faecal pellets (Manno C. et al., 2010). The faecal pellets flux of *Limacina helicina* in the Ross Sea contributed on average 19% of the particulate organic carbon (POC) flux, with the highest contribution of up to 30% (Manno C. et al., 2010). Measured production rate in the laboratory conditions ranged from 6.1 ±1.3 to 10.9 ±2.1 faecal pellets day^{-1} $ind.^{-1}$, while the production rate calculated from the ratio of *Limacina helicina* specimen abundance versus total number of faecal pellets collected in sediment traps was 19 faecal pellets day^{-1} (Manno C. et al., 2010). Sinking velocities of faecal pellets are determined by their size, shape and their density (Komar P.D. et al., 1981; Taghon G.D. et al., 1984). While the size and shape are characteristic for the producer, the density of faecal pellets varies according to the quality and quantity of ingested food (Bruland K.W. and Silver M.W., 1981; Yoon W. et al., 2001). Yoon W. et al. (2001) recorded sinking rates of pteropod *Clio* spp. between 65 and 206 m day^{-1}. Furthermore, Bruland K.W. and Silver M.W. (1981) determined faecal pellets sinking rates of pseudothecosome *Corolla spectabilis* to be ranging from 440-1800 m day^{-1} (std= 423 m day^{-1}), which is on the higher end of the range compared with other zooplankton groups, such as copepods. This makes the contribution of pteropods to downward transport of biogenic materials by their faecal pellets important (Bruland K.W. and Silver M.W., 1981; Komar P.D. et al., 1981).

The soft tissues of pteropods also contribute to the organic carbon flux. According to Accornero A. et al. (2003), the soft parts of *Limacina helicina* specimen in the Ross Sea contributed 53 % to the annual particulate organic carbon. Bednaršek N. et al. (2012a) determined the contribution of organic (TOC) versus inorganic (TIC) carbon in *Limacina helicina to be* 73% and 27%, respectively. To compare the TOC/TIC ratio of Bednaršek N. et al. (2012a) with the results from Gannefors C. et al. (2005) for the Arctic *Limacina helicina* specimen, the measurements of ash-weight, ash–free weight and dry weight of pteropod specimen by the latter study were recalculated (Annex B). In all tested specimen, TOC contributed a greater share to total carbon than TIC (Annex B). Therefore, even though the TOC/TIC ratio is expected to be different in other species and in specific life stages of pteropods, the results implied that organic carbon substantially outweighed inorganic carbon contribution to the carbon flux. The estimates of possible combined contribution of pteropod soft parts and faecal pellets to the total organic carbon export were as high as 72% (Manno

C. et al., 2010). In the Ross Sea, Collier R. et al. (2000) measured POC of 5-10 mmol C m^{-2} day^{-1} (60-120 mg C m^{-2} day^{-1}) in austral autumn, mainly due to the occurrence of *Limacina helicina.*

Moreover, migratory pteropods feed in the surface layers during the night and migrate into greater depths during the day, where they excrete carbon rich waste products (faecal pellets, respiratory CO_2) thus contributing additionally to transport of organic carbon via biological pump from the surface to ocean interior (Accornero A. et al., 2003; Honjo S. et al., 2008; Maas A.E. et al., 2012b). Last but not least is the role of sinking shells of dead pteropods acting as the ballast material and thus increasing the efficiency of downward transport of particulate organic matter trough the water column, which results in deeper remineralisation of organic matter (Armstrong R.A. et al., 2002; Hoffman M. and Schnellnhuber H.-J., 2008).

2.5.2.2 Inorganic Carbon export

Being calcifying organisms, pteropods are a part of ocean carbonate system and involved in inorganic carbon export out of the surface waters into the deeper ocean and thus in the ocean-atmosphere CO_2 feedback loops (Fabry V.J., 1989; Tsurumi M. et al., 2005; Hood R.R. et al., 2006; Fabry V.J. et al., 2008). The calcification of pelagic organisms represents one of the mechanisms reducing ocean surface alkalinity, which decreases the potential of surface water for the uptake of atmospheric CO_2 (Feely R.A. et al., 2004; Sarmiento J.L. and Gruber N., 2004). The result of $CaCO_3$ percipitation is actually formation of CO_2, due to the following reaction:

$$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + H_2O + CO_2. \qquad \text{(Eq. 1)}$$

However, as mentioned before, the mineral ballast (particulate inorganic carbon) produced by pelagic calcifiers (the carbonate pump) increases the export flux of particulate organic matter into deep ocean, strengthening the biological carbon pump (Armstrong R.A. et al., 2002; Sarmiento J.L. and Gruber N., 2004; Hoffman M. and Schnellnhuber H.-J., 2008).

Thecosomatous pteropods are one of the important planktonic producers of $CaCO_3$ in the global oceans (Fabry V.J., 1989; Hood R.R. et al., 2006; Fabry V.J. et al., 2008; Gangstø R. e tal., 2008). However, the contribution of pteropods to global pelagic carbonate production was until recently considered as minor in comparison with production of coccolithophores and foraminifers (Schiebel R., 2002). In regions where coccolithophores and foraminifers were abundant, pteropods were observed to be a minor contributor to total $CaCO_3$ production; Fabry V.J. (1989) estimated the pteropod contribution to total annual $CaCO_3$ production in the subarctic was only 3-13%, the major contributor being coccolithophores and foraminifers. On a global scale, aragonite production by pteropods was estimated to constitute at least 12% of the total carbonate flux worldwide (Berner R.A. and Honjo S., 1981). The results of more recent modelling studies however suggest the contribution of pteropods to total global pelagic $CaCO_3$ production could be as much as 35% (Gangstø R. et al., 2008). It was previously suggested that most of the aragonite production takes place in polar and sub-polar regions (Lalli C.J. and Gilmer R.W., 1989), in the environments such as the Southern Ocean regions and the Arctic Ocean where other producers are less abundant (Holligan P.M. et al., 2010). In such areas, the contribution of pteropods to $CaCO_3$ flux can be much higher (up to >50%; Lalli C.J. and Gilmer R.W., 1989), more relevant and comparabale with the estimates for the other open ocean peagic calcifiers (Accornero A. et al., 2003; Tsurumi M. et al., 2005; Bednaršek N. et al., 2012a). Recent moddeling studies estimated that a larger (approximately 40%; possibly overestimated) part of the aragonite production also occurs between 0-20° (Gangstø R. et al., 2008).

Aragonite shells of thecosomatous pteropods discarded by successful predators and the shell vertical fluxes of seasonal die-offs contribute to carbon flux to deeper water layers

(Tsurumi M. et al., 2005; Hunt B.P.V. et al., 2008). The sinking velocity of empty pteropod shells was approximated between 864 – 1210 m day^{-1} (Lalli C.M. and Gilmer R.W., 1989). The magnitude of the flux of pteropods is correlated to the standing stock of the living population, which depends on the food abundance (Almogi-Labin A. et al., 1988). The total pteropod flux changes seasonally, often being the lowest in autumn and highest in spring, which generally applies to majority of pteropod species, although each one also has its own characteristic flux pattern variations (Almogi-Labin A. et al., 1988). If the shell flux is high, they can form large deposits of aragonite rich sediments on the ocean floor (pteropod oozes – sediments with 30% share of pteropod shells) (Lalli C.M. and Gilmer R.W., 1989; Honjo S. et al., 2000, 2004; Hunt B.P.V. et al., 2008). The sediments are usually found in shallow depths and deeper only in the subtropical and tropical areas (at <2800 m in Atlantic and <500 m in Pacific), where aragonite saturation extends into greater depths (Almogi-Labin A. et al., 1988; Orr C.J. et al., 2005; Hunt B.P.V. et al., 2008). This is due to the relatively shallow aragonite horizon above which aragonite is thermodynamically stable and which shoals with the falling temperature, in correlation with depth and pH (Feely R.A. et al., 2004; Orr C.J. et al., 2005; Fabry V.J. et al., 2008; Hunt B.P.V. et al., 2008). If the aragonite shells sink below aragonite saturation horizon, they dissolve into bicarbonate ions, incorporating CO_2 in the process, consequently increasing alkalinity and thus enhancing capacity of the deep ocean for CO_2 storage (Byrne R.H. et al., 1984; Feely R.A. et al., 1988; Iglesias-Rodrigues M.D. et al., 2002).

2.6 Ocean acidification and the change in $CaCO_3$ saturation state

Ocean acidification and its potential effects on pteropods, obtained through experimental and observational studies are closely described in this chapter, because the impacts of ocean acidification present a major threat for pteropods as well as other calcifying organisms in the globally changing marine environment (Fabry V.J. et al., 2008; Doney S.C. et al., 2009). With the input of anthropogenic CO_2, pteropod shell dissolution is the main reason for their vulnerability to ocean acidification (Orr C.J. et al., 2005; Fabry V.J. et al., 2008; Lischka S. et al., 2011; Comeau S. et al., 2010b; Bednaršek N. et al., 2012b).

2.6.1 Changes in ocean chemistry

When CO_2 dissolves in seawater, carbonic acid (H_2CO_3) is formed. Most of the H_2CO_3 quickly dissociates into hydrogen ion (H^+) and bicarbonate ion (HCO_3^-). H^+ can then react with carbonate ions (CO_3^{2-}) and they form HCO_3^-. The net effect of adding CO_2 to seawater is thus increased concentration of H_2CO_3, HCO_3^- and H^+ and at the same time decreased concentration of CO_3^{2-} and consequently lowering of pH (Feely R.A. et al., 2004; Fabry V.J. et al., 2008; Eq. 2).

$$CO_2 + CO_3^{2-} + H_2O \rightleftarrows 2HCO_3^- \qquad \text{(Eq. 2)}$$

Deeper colder waters are naturally depleted in CO_3^{2-} relative to the surface based on thermal dynamics of carbonate buffering system in the seawater, which makes cold waters of the Arctic Ocean naturally low in carbonate ion concentrations (Juranek L.W. et al., 2003; Orr C.J. et al., 2005). The supply of CO_3^{2-} in the carbonate buffering system is primarily from geological erosion, which is a slow process (Widdicombe S. and Spicer J.I., 2008).

The $CaCO_3$ saturation state (Ω) is a product of Ca^{2+} and CO_3^{2-} concentrations divided by stoichiometric solubility product (K_{sp}^*) for either aragonite or calcite (Feely R.A. et al., 2004):

$$\Omega = [Ca^{+2}]\,[CO_3^{2-}]/\,K_{sp}^* \qquad \text{(Eq. 3)}$$

Calcium concentration is estimated from salinity, whereas carbonate ion concentration is estimated from dissolved inorganic carbon (DIC) and total alkalinity (Feely R.A. et al., 2004). Changes in [CO_3^{2-}] are consequently directly reflected in the change of Ω (Feely R.A. et al., 2004; Fabry V.J. et al., 2008).

Pteropods need carbonate ions to produce their aragonite shells (Fabry V.J., 1989). The solubility of $CaCO_3$ increases with decreasing temperature and as a result, saturation states are generally highest in tropical and subtropical regions (Orr C.J. et al., 2005; Fabry V.J. et al., 2008). The $CaCO_3$ percipitation for shell formation was proposed possible for pteropods until aragonite saturation of 0.64 (Comeau S. et al., 2010a). However, the water with aragonite saturation value Ω_{ara} <1 is corrosive to pteropod shells (Orr C.J. et al., 2005; Fabry V.J. et al., 2008). Bednaršek N. et al. (2012b) showed a dissolution of shells occurs in near saturation conditions, at Ω_{ara}= 0.97 ±0.11.

The ocean uptake of anthropogenic CO_2 is altering seawater chemistry – elevated partial pressure of CO_2 (pCO_2) is causing the water pH and calcium carbonate ($CaCO_3$) saturation state to decrease. This phenomenon is called ocean acidification and its magnitude in the future, particularly at the ocean surface, is directly proportional to the amount of CO_2 emitted into the atmosphere (Gruber N., 2011). Due to ocean acidification, the carbonate (aragonite) saturation horizon is expected to shoal in many regions, particularly in high latitudes (Orr C.J. et al., 2005; Fabry V.J. et al., 2008). Polar oceans are expected to reach aragonite undersaturation first due the naturally low saturation state in these areas (Orr C.J. et al., 2005; Gruber N., 2011). Parts of the Arctic Ocean are to become undersaturated during the next decade (Steinacher M. et al., 2009), followed by Southern Ocean, becoming undersaturated in the second half of this century, although seasonally in certain regions already in two decades (Orr C.J. et al., 2005; McNeil B.I. and Matear R.J., 2008). If the acidity of high latitude oceans increases and the waters become undersaturated with regard to $CaCO_3$, which is predicted to happen in the matter of decades (Orr C.J. et al., 2005), pteropods in the high-latitude regions will be one of the first to experience the impacts of the changed ocean chemistry conditions (Feely R.A. et al., 2004; Orr C.J. et al., 2005; Fabry V.J. et al., 2008; McNeil B.I. and Matear R.J., 2008; Comeau S. et al., 2011). Bednaršek N. et al. (2012b) showed that dissolution is already underway for the pteropods in the Southern Ocean.

2.6.2 Impacts of acidification (lower pH, elevated pCO_2, shoaling aragonite saturation horizons) on pteropods

Higher levels of CO_2 in the marine environment can potentially influence metabolic rates of pteropods. 20% suppression in oxygen consumption was measured for pteropod *Limacina helicina antarctica* at 1000 ppm pCO_2 and -1.8°C (Seibel B.A. et al., 2012). Maas A.E. et al. (2012a) recorded a significantly reduced oxygen consumption and ammonia excretion in non-migratory species *Diacria quadrientata* collected in tropical region of the Pacific Ocean, when exposed to high (1000 ppm) CO_2 concentration. Conversely, metabolic rates of pteropod species *Hyalocylis striata, Clio pyramidata, Cavolinia longirostris* and *Creseis virgula* (collected in the same region), naturally migrating into oxygen minimum zones, were not affected by short term exposure to elevated CO_2 levels (Maas A.E. et. al., 2012a). Comeau S. et al. (2010a) recorded elevated metabolic rate in *Limacina helicina* from the Arctic under increasing pCO_2, although only at simultaneously elevated temperature (but not at the control temperature), demonstrating a response of metabolic activity to combined effects of pCO_2 and temperature. It is possible that some species of pteropods or specimen of the same species living in different regions are physiologically adapted to various natural habitat conditions, such as different pCO_2 levels, and may consequently cope differently with the ocean acidification (Byrne M., 2011; Maas A.E. et al., 2012a). However, the response to

chronic exposure to ocean acidification is presumably negative also for the species adapted to short-term elevated CO_2 levels exposure (Maas A.E. et al., 2012a).

With their highly soluble aragonite shells, thecosomatous pteropods are highly susceptible to ocean acidification and are expected to be heavily impacted by aragonite undersaturation, especially in the polar regions (Orr C.J. et al., 2005; Seibel B.A. et al., 2007; Fabry V.J. et al., 2008; Bednaršek N., 2012b). The available data indicate pteropods demonstrated reduced calcification rates and dissolution of aragonite shells when exposed to elevated pCO_2 and decreasing pH and CO_3^{2-} concentration in the undersaturated condtions, i.e. when $\Omega_{ara} < 1$ (Feely R.A. et al., 2004; Orr C.J. et al., 2005; Fabry V.J. et al., 2008; Bednaršek N. et al., 2012a). The experiments on Arctic *Limacina helicina* exposed to 780 ppm pCO_2 resulted in 28% decrease in calcification rate (Comeau S. et al., 2009). In the study of Comeau S. et al. (2010a) calcification of the Arctic *Limacina helicina* also declined with elevated pCO_2 (up to 1020 ppm) at control (0°C) and elevated (4°C) temperature. However, Comeau S. et al. (2010a) found no synergistic effect of elevated pCO_2 and temperature. In addition, the results demonstrated that *Limacina helicina* precipitated aragonite in aragonite undersaturated ($\Omega_{ara}<1$) conditions (at higher temperature, 4°C), although the shell dissolution continued at the same time (Comeau S. et al., 2010a). Similarly, Lischka S. et al. (2011) recorded continuous (although significantly reduced) shell growth of *Limacina helicina* specimen at $\Omega_{ara}<1$, but there was no apparent interaction between temperature and elevated pCO_2. It is thus not yet clear if pteropods can achieve positive balance between calcification and dissolution in the undersaturated environment and at the same time sustain development, reproduction and accumulation of energy reserves (Comeau S. et al., 2010a; Lischka S. et al., 2011). Other experiments showed that even when pteropods were still alive, the dissolution of shells occured if pteropods were subjected to a certain level of undersaturation with respect to aragonite (Orr C.J. et al., 2005; Comeau S. et. al. 2010b; Lischka S. et al., 2011; Bednaršek N. et al., 2012b)

Due to increased pCO_2 levels in the seawater, the dissolved CO_2 diffuses more readily across animal surfaces, it crosses biological membranes and reacts with intra- and extracellular fluids (Fabry V.J. et al., 2008; Maas A.E. et al., 2012a). Consequently, animals have to face the acid-base imbalance in their bodies (internal acidification), which can influence different physiological processes (Widdicombe S. and Spicer J.I., 2008) and as a result, oxygen transport capacity can be reduced (Fabry V.J. et al., 2008; Pörtner H.-O. 2008, 2010). Most marine animals have mechanisms to control their internal pH balance, but those are often energetically costly (Fabry V.J. et al., 2008; Wood H.L. et al., 2008). The capacity to compensate for pH changes in the environment differ among different species determining different levels of tolerance for environmental pH changes (Maas A.E. et al., 2012a).

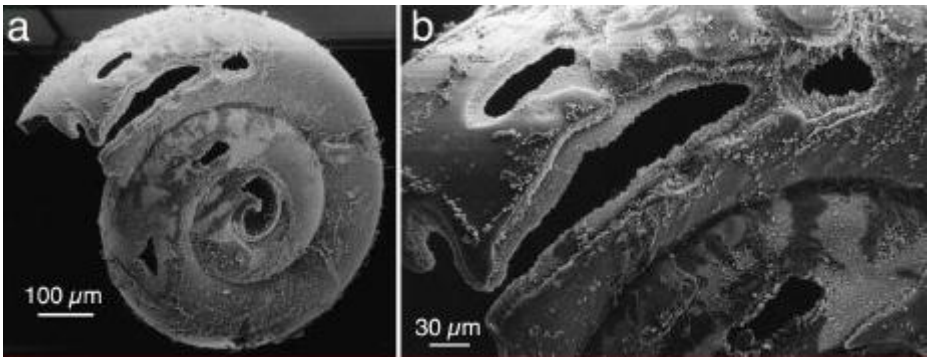

Figure 4: *Results of shell dissolution in arctic juvenile Limacina helicina, exposed to elevated pCO_2 levels (1100 ppm, at 3°C) for 29 days (Scanning electron micrographs; Lischka S. et al., 2011: 923).*

Response to acidified conditions is not only species-specific, but is also expected to differ among different life stages of the same species (Byrne M., 2011). A higher vulnerability to elevated CO_2 levels was especially evident in the early life stages of many species of calcifying marine organisms, including pteropods (Byrne M., 2011). The shells of juvenile *Limacina helicina antartica* dissolve more rapidly than adult shells, making juveniles especially vulnerable to aragonite undersaturation (Bednaršek N., 2010). Additionally, as veliger gymnosomes and pseudothecosomes posses shells as well, these life stages could thus also be impacted (Fabry V.J. et al., 2008). Larvae of Mediterranean pteropod *Cavolinia inflexa* maintained at low pH values 7.82 (857 ppmv pCO_2) and 7.51 (1713 ppmv pCO_2), showed malformations in larvae shell growth and complete absence of larvae shells, respectively (Comeau S. et al. 2010b). However, the shell-less larvae were viable and their normal development was observed (Comeau S. et al., 2010b). Increased shell degradations and reduced shell size in juvenile specimen of Arctic *Limacina helicina* exposed to elevated (up to 1150 ppm) pCO_2 was also confirmed by Lischka S. et al. (2011) (Figure 4).

To conclude, decreased calcification with increased dissolution would presumably compromise the fitness of pteropods and could shift the competitive advantage towards non-calcifiers (Fabry V.J. et al., 2008). The short term exposure to udersaturation may pose a higher susceptibility to predation (Feely R.A. et al., 2004), whereas long term and chronic undersaturation could threaten long-term survival of pteropods (Bednaršek N., 2012b; Comeau S. et al., 2011; Maas A.E. et al., 2012a). Whether net rates of calcification can still exceed shell dissolution will likely depend on the degree of $CaCO_3$ undersaturation and the duration of the exposure to undersaturated conditions (Fabry V.J. et al., 2008; Maas A.E. et al., 2012a). The resilience of different species of pteropods and their life stages to long-term changes in pH due to ocean acidification remains to be fully explored and assessed. Data available on pteropod responses to ocean acidification generally suggest the reduction in calcification, but the number of species tested is too small to draw general conclusions of the responses of pteropods as a group – species specific responses are likely as some might be more susceptible to changes than the others and some capable of adapting better from the others (Fabry V.J. et al., 2008; Doney S.C. et al., 2009; Maas A.E. et al., 2012a). Furthermore, additional experiments and observations are needed to explore the interactive effects of $CaCO_3$ undersaturation, temperature changes, oxygen levels and nutrition availability on different species of pteropods in different life stages (Byrne M., 2011; Lischka S. et al., 2011) and over longer periods (e.g. four seasons; Seibel B.A. et al., 2012).

3 METHODS

3.1 Data collection

An extensive search of the available observational data on pteropod abundance and biomass records in the world oceans was carried out. That included a review of scientific publications and already published or online available databases, from which the records of abundance/biomass data of orders Gymnosomata (naked pteropods) and Thecosomata (shelled pteropods) were extracted.

The majority of data was obtained from the three online databases: PANGEA archive, ZooDB – Zooplankton database and NMFS-COPEPOD (The Global Plankton Database). The scientific papers and databases used as data sources are listed in Table 1. The output of this work generated 25 939 data points that are now available to download as an online data collection at PANGEA archive (http://doi.pangaea.de/10.1594/PANGAEA.777387).
Each data point in the created dataset, consisting of 25 939 data points, included the following information:

- Time of sampling (Year, Month, Day)
- Location of sampling (Longitude, Latitude)
- Sampling depth (m)
- Pteropod classification (Taxons)
- Pteropod abundance (ind. m^{-3}) and/or pteropod biomass (mg m^{-3})
- Mesh size (µm; Sampling strategy)
- Data source (Reference)

The majority of data points were records of pteropod abundance, with only a few studies originally reporting the biomass values, the latter being specifically distinguished in the collected database from the calculated biomass values.

***Table 1**: The list of data contributors in alphabetical order, with the two major online databases listed at the end of the list.*

Entry No.	Principal Investigator	Database	Year (data collection)	Region
1	Andersen V. (1997)	PANGEA	1991-1992	NE tropical Atlantic
2	Bednaršek N. et al. (2012a)	-	1996-2010	Southern Ocean (Scotia Sea)
3	Bernard K.S. and Froneman P.W. (2005)	-	2004	Southern Ocean (west-Indian sector of the Polar Frontal Zone)
4	Blachowiak-Samolyk K. et al. (2008)	-	2003	Arctic (N Svalbard waters)
5	Boysen-Ennen E. et al. (1991)	-	1983	Antarctica (Weddell Sea)
6	Broughton E.A., Lough R.G. (2006)	-	1997	North Atlantic (Georges Bank)
7	Clarke C. and Roff J.C. (1990)	-	1986	Caribbean Sea (Lime Cay)
8	Daase M. and Eiane K. (2007)	-	2002-2004	Arctic (N Svalbard waters)
9	Dvoretsky V.G. and Dvoretsky A.G. (2009)	-	2006	E Barents Sea (Novaya Zemlya)
10	Elliot T. D. et al. (2009)	-	2006-2007	Antarctica (McMurdo Sound)
11	Fernandez de Puelles M. L. et al. (2007)	-	1994-2003	Western Mediterranean
12	Flores H. et al. (2011)	-	2004-2008	Southern Ocean (Lazarev Sea)
13	Foster B.A. (1987)	-	1985	Antarctica (McMurdo Sound)
14	Froneman P.W. et al. (2000)	-	1998	Southern Ocean (Prince Edward Archipelago)
15	Hunt B.P.V. and Hosie G.H. (2006)	-	2001-2002	Southern Ocean (south of Australia)
16	Koppelmann R. et al. (2004)	PANGEA	1999	Eastern Mediterranean Sea
17	Marrari M. et al. (2011)	-	2001/2002	W Antarctic (Marguerite Bay)
18	Mazzocchi M.G. (1997)	PANGEA	1991-2002	Eastern Mediterranean Sea
19	Mileikovsky S.A. (1970)	-	1966	North Atlantic, subarctic and North Pacific Ocean
20	Moraitou-Apostolopoulou M. et al. (2008)	PANGEA	1994	Eastern Mediterranean Sea
21	Mousseau L. et al. (1998)	-	1991-1992	NW Atlantic (Scotian Shelf)
22	Nishikawa J. (2007)	-	2000-2002	Pacific Ocean (Sulu Sea, Celebes Sea, South China Sea)
23	Pakhomov E.A. and Perissinotto E.A (1997)	-	1993	Southern Ocean (Subtropical Convergence)
24	Pane L. et al. (2004)	-	1995	Antarctica (Ross Sea)
25	Ramfos A. et al. (2008)	PANGEA	2000	Eastern Mediterranean

It continues.

Continuing.

Entry No.	Principal Investigator	Database	Year (data collection)	Region
26	Rogachev K.A. et al. (2008)	-	2004	W Pacific Ocean (Academy Bay, Sea of Okhotsk)
27	Schalk P. H. (1990)	-	1984-1999	Indo-Pacific waters (E Banda Sea, W Arafura Sea)
28	Schnack-Schiel S., Cornils A. (2009)	PANGEA	2005	Pacific Ocean (Java Sea)
29	Siokou-Frangou I. et al. (2008)	PANGEA	1987-1997	Eastern Mediterranean
30	Solis N.B. and von Westernhagen N. B. (1978)	-	1972	Philippines (Hilutangan Channel)
31	Swadling K.M. et al. (2011)	-	2004-2008	E Antarctica (Dumont d'Urville Sea)
32	Volkov A.F. (2008)	-	1984-2006	Okhotsk Sea, Bering Sea, NWP
33	Ward P. et al. (2007)	-	2004-2005	Southern Ocean (S&W of Georgia)
34	Wells F.E. Jr. (1973)	-	1972	N Atlantic Ocean (Barbados)
35	Werner I. (2005)	-	2003	Arctic (W Barents Sea)
36	Wormuth J.H. (1985)	-	1975-1977	N Atlantic Ocean (NW Sargasso Sea)
37	Zervoudaki S. et al. (2008)	PANGEA	1997-2000	Eastern Mediterranean
38	NOAA (National Oceanic and Atmospheric Administration) (2011)	COPEPOD – The global plankton database	1953-2001	Global dataset
39	Ohman M.D. (2011)	ZooDB – Zooplankton database	1951-1999	Pacific Ocean (Southern and Central California)

3.2 The primary data processing

With the aim of describing pteropod biomass in the global world oceans, all the abundance values from the dataset were converted into biomass. Prior the conversion, collected data were pre-checked and sorted to avoid potential errors in the global pteropod biomass estimates in the later stages.

Different names of pteropod species were uniformed for data to be sorted to the common species level. Furthermore, there were several studies, where repeated sampling was conducted at the same location, time and depth. In such cases, where a complete overlap of data was present (excluding mesh size, which was not taken into account), the data points were summed up to non-overlaying 14 136 data points. Moreover, zero biomass values were included as biologically valid data points in the dataset.

The abundance/biomass data was included in the dataset regardless of the sampling methodology and equipment used to obtain the data in the initial study, such as different

mesh sizes and sampling strategies. Thus, it was important to include all available information on mesh size, the type of sampling strategy in the dataset in order not to introduce bias when analysing data.

3.3 Biomass conversion methodology

A set of conversion equation to convert pteropod abundance to biomass was chosen from the literature, with the Eq. (4) as the underlying principle:

Stock biomass = Mean Dry Weight of the population (mg)*Abundance (ind. m^{-3}) (Eq. 4).

Firstly, mean dry weight of the pteropod population was calculated, further multiplied with the abundance, generating the required carbon stock biomass values. In cases, where the data sources initially reported biomass values, these values were not recalculated using the algorithm divides, but were kept in the original values. Additional calculations were performed to transform the stock biomass values to carbon biomass values and to uniform the units to C mg m^{-3}.

3.3.1. Wet weight and dry weight calculations

Wet or dry weight values were calculated using species- or group-specific length-to-weight conversion equations.

For the species where specific length-to-weight conversion equations were not available, a more general approach for length-to-weight conversion was used - a method similar to the one previously employed by the GLOBal ocean ECosystems dynamics (GLOBEC) data management program. In GLOBEC, wet weights (WWs) of different pteropod families were calculated based on their specific body geometry and length (Little W. S. and Copley N. J., 2003). The length-WW biomass conversion equations used in the GLOBEC program were formulated to cover the barrel shaped *Clione* family of naked pteropods, cone shaped family of *Styliola*, low-spire (globular) family of *Limacina* spp., and pyramidally shaped family of *Clio* spp. (Little W.S. and Copley N.J., 2003). Taking into account available GLOBEC conversions for four different geometrical shapes of pteropods (Little W.S. and Copley N.J., 2003), this metrics was further extended to pteropod families sharing similar body geometry. Based on different shapes, four different groups were formed with four different aligning length-to-WW conversions (Eq.5-8) (Little W.S. and Copley N.J., 2003):

Barrel/oval shaped (naked): WW=10^(2.533*log(L)-3.89095)*10^3 Eq. (5),

Triangular/pyramidal shaped (shelled): WW= 0.2152*L^2.293 Eq. (6),

Round/cylindrical/globular shaped (shelled): WW=0.000194*L^2.5473 Eq. (7),

Cone/needle/bottle shaped (shelled): WW= PI*L^3*3/25 Eq. (8),

where L represents length (mm) and WW represents wet weight (mg). In Eq. (5), Eq. (6) and Eq. (7) a regression of length and weights (mg) was derived from the population of animals, whereas Eq. (8) is based on the shape of the organism and a density of 1 was assumed (Little W.S. and Copley N.J., 2003).

Where species or families of sampled pteropods in the abundance records were not specified, but were classified on order or sub-order level (e.g. Thecosomata, Gmynosomata, Pteropoda), a more general equation by Davis C.S. and Wiebe P.H. (1985) was used:

WW=0.2152*L^2.293 Eq. (9).

All the obtained WWs were subsequently converted to dry weights (DWs) using Davis C.S. and Wiebe P.H. (1985) equation:

DW=WW*0.28 Eq. (10).

One exception where multiple length-to-weight conversion equations existed was *Limacina helicina.* In each one of the three existing studies a different equation was used for the length to DW relationship of *Limacina helicina:*

$\log DW = 0.685\ L^{-2.222}$ Eq. (11), Fabry V.J. (1989)
$DW = 0.257\ L^{2.141}$ Eq. (12), Gannefors C. et al. (1995)
$DW = 0.1365\ L^{1.501}$ Eq. (13), Bednaršek N. et al. (2012a).

To make further comparison of *Limacina* data points from different studies feasible, a comparison between the three studies (Fabry V.J. et al. (1989), Gannefors C. et al. (2005), Bednaršek N. et al. (2012a)) was conducted, focusing on the length-to-weight correlations (Bednaršek N. et al., 2012c). The performances of the equations across a uniform range of *Limacina* specimen sizes (0.01 – 50 mm) were evaluated (Bednaršek N. et al., 2012c). The equation from Fabry V.J. (1989) turned out to be unsuitable for calculating DW in the size range of the present study, because the DW results were optimal for the size range between 1 and 4 mm, but became exponentially large at shell diameters above this range. The equations from Gannefors C. et al. (1995) and Bednaršek N. et al. (2012a) had a similar performance and offered realistic results of DW for the larger shell diameter sizes, relevant for this study. The equation from Bednaršek N. et al. (2012a) was chosen as the most suitable for calculating the DWs of *Limacina helicina* in the newly created dataset of pteropod biomass because the estimates of DW between 1 and 4 mm of shell diameter were in between the estimates of the Fabry V.J. (1989) and Gannefors C. et al. (1995). In this algorithm DW increases exponentially with the shell length, with an allometric exponent of 1.501 (Bednaršek N. et al., 2012a).

Moreover, to calculate DW of *Clione* spp. in the dataset, an equation (Eq. 14) from Böer M. et al. (2005) was used:

$DW=1.6146^{e0.0088*L}$ Eq. (14).

All the pteropod groupings and aligned specific equations used to calculate WWs and DWs for each group or species are listed in Table 2.

Table 2: *Length-to-weight conversion equations for different pteropod species and groups based, on their geometric shapes.*

Taxon	Group	Equation source	Conversion	Equation name (e.g. in GLOBEC)	Equation (size-weight relationship)	Conversion	Davis C.S and Wiebe P.H. (1985) Equation
Limacina helicina	Round/cylindrical/ globular	Bednaršek N. et al., 2012	Diameter→ DW		DW=0.137*L^1.5005		
Limacina spp.	Round/cylindrical/ globular	GLOBEC	Diameter→ DW	Pteropod1 (low-spire: Limacina)	$DW=0.000194xL^{2.5473}$	WW→DW	WW*0.28
Clione spp.	Barrel/oval-shaped (naked)	Böer M. et al., 2005	Length→ WW		$DW=1.6146^{e0.0088*L}$		
Hyalocylis spp.	Cone-shaped (+needle/tube/bottle)	GLOBEC	Length→ WW	Pteropod (cone-shaped: Styliola)	WW=PI*L^3*3/25	WW→ DW	WW*0.28
Styliola spp.	Cone-shaped (+needle/tube/bottle)	GLOBEC	Length→ WW	Pteropod (cone-shaped: Styliola)	WW=PI*L^3*3/25	WW→ DW	WW*0.28
Spongiobranchaea spp.	Barrel/oval-shaped (naked)	GLOBEC	Length→ WW	Pteropod (naked: Clione)	WW=10^(2.533*log(L) -3.89095)*10^3	WW→ DW	WW*0.28
Pneumodermopsis spp.	Barrel/oval-shaped (naked)	GLOBEC	Length→ WW	Pteropod (naked: Clione)	WW=10^(2.533*log(L) -3.89095)*10^3	WW→ DW	WW*0.28
Paedoclione spp.	Barrel/oval-shaped (naked)	GLOBEC	Length→ WW	Pteropod (naked: Clione)	WW=10^(2.533*log(L) -3.89095)*10^3	WW→ DW	WW*0.28
Cavolinia spp.	Triangular/pyramidal	GLOBEC	Length→ DW	Pteropod (Clio)	WW=0.2152*L^2.293	WW→ DW	WW*0.28

It continues.

Continuing.

Taxon	Group	Equation source	Conversion	Equation name (e.g. in GLOBEC)	Equation (size-weight relationship)	Conversion	Davis C.S and Wiebe P.H. (1985) Equation
Clio spp.	Triangular/pyramidal	GLOBEC	Length→ WW	Pteropod (Clio)	WW=0.2152*L^2.293	WW→ DW	WW*0.28
Creseis spp.	Cone-shaped (+needle/tube/bottle)	GLOBEC	Length→ WW	Pteropod (cone-shaped: Styliola)	WW=PI*L^3*3/25	WW→ DW	WW*0.28
Cuvierina spp.	Cone-shaped (+needle/tube/bottle)	GLOBEC	Length→ WW	Pteropod (cone-shaped: Styliola)	WW=PI*L^3*3/25	WW→ DW	WW*0.28
Diacria spp.	Triangular/pyramidal	GLOBEC	Length→ WW	Pteropod (Clio)	WW=0.2152*L^2.293	WW→ DW	WW*0.28
Thecosomata	Shelled	Davis C.S. and Wiebe P.H. (1985)	Length → WW		WW=0.2152*L^2.293	WW→ DW	WW*0.28
Gymnosomata	Naked	Davis C.S. and Wiebe P.H. (1985)	Length → WW		WW=10^(2.533*log(L) -3.89095)*10^3	WW→ DW	WW*0.28
Pteropoda	Shelled	Davis C.S. and Wiebe P.H. (1985)	Length → WW		WW=0.2152*L^2.293	WW→ DW	WW*0,28

3.3.2 Length estimations

Prior to using the length-to-weight conversion equation, information on the lengths of selected species was required. Where information on the length was not available, the approximate sizes of all different pteropod species were estimated on the sizes found in Marine Species Identification Portal (http://species-identification.org/). The information available on the Marine Identification Portal was mostly in the form of maximum size (length/diameter) of the adult form of specific pteropod species. Consequently, the lengths used in this study (Annex A) also represented maximum lengths, which might overestimated the calculated biomasses (described in chapter 4.7.3 in Results section). With the purpose of at least partially avoiding overestimations, especially in the case of very high pteropod abundance recordings, specific approaches to calculate the biomass of juvenile stages, as well as the biomass of pteropod groups above species level (families, orders, classes) were used as explained below.

The created pteropod database contained 283 entries (2% of the database) where abundance data represented juvenile life stages (larvae and veligers). The juveniles were categorized into specific group with the same equations to calculate WW as for the adult specimens. However, the length of the juveniles was estimated to be only 10% of the average adult size, which is based on the comparison of average juvenile and adult sizes performed specifically for this study (Bednaršek N., person. comm.).

Where the classification of pteropods was on the level of orders (Thecosomata and Gymnosomata), sub-orders (Euthecosomata) or groups (Pteropoda as a classification group) the animals were classified as adults and the lengths calculated as average of the groups of lower taxonomic levels. For example, the length for the order Gymnosomata was calculated as the average of length values of genuses *Paedoclione, Clione, Pneumodermopsis* and *Spongiobranchaea* (Annex A). Accordingly, the length of genus *Clione* was calculated as the average of lengths of different species of this genus (Annex A). In this way, a single species did not overestimate the group-specific length. Finally, the length used in conversion equations for Pteropoda was the average of lengths of orders Thecosomata and Gymnosomata (Annex A).

3.3.3 Stock biomass and carbon biomass calculation

The final step in the biomass conversion was multiplying the obtained DWs with the abundance data to procure the required biomass values. Additionally, the stock (DW) biomass was later transformed to carbon (organic and inorganic) biomass (mg m^{-3}) using the conversion factor by Larson R.J. (1986), which assumed a dry weight to carbon conversion factor of 0.25, following Eq. 15:

Carbon biomass (mg m^{-3}) = Dry weight biomass (mg m^{-3}) x 0.25 (Eq. 15).

3.4 Statistical analysis of biomass data

The outcome of using the conversion methodology was a raw dataset, containing parameters, such as location, depth, time, abundance, stock biomass, carbon biomass, mesh sizes, additional information on sampling methodology and the references.

Subsequently, data file was gridded onto 360 x 180° grid, with vertical resolution of 33 WOA depth levels, done by Dr. Erik T. Buitenhuis from the University of East Anglia. Conversion of data to NetCDF file format was done for the ease of use in model evaluation exercises (Buitenhuis E.T. et al., 2012a). More specific information about the gridding can be found in Buitenhuis E.T. et al. (2012a). Both, the full (raw) data set and the gridded NetCDF data file are publicly available from the PANGAEA World Data Centre (http://www.pangaea.de/search?&q=maredat), together with the other ten PFT data files.

The analysis of the obtained biomass values in the gridded data file were executed in Matlab as a collaborative work between myself and my thesis supervisor, Dr. Nina Bednaršek.

Since shelled pteropods (Thecosomes) represent an important contribution to the inorganic carbon flux in the oceans (see chapter 2.5.2.2) the knowledge on the pteropod global distribution can provide an insight into the global carbonate budgets. For this, carbon biomass of shelled pteropods only was calculated in order to subsequently calculate the carbonate (inorganic carbon) budget presented by pteropods. To calculate the total inorganic carbon content percentage, Eq. (16) was used:

TIC (%) = TC (%) – TOC (%) Eq. (16)

Furthermore, assuming all inorganic carbon is in the form of calcium carbonate, Eq. (17) was used to express total inorganic carbon as a calcium carbonate in percentage ($CaCO_3$, %):

CaCO3 (%) = [TC (%) – TOC (%)] x 8.33 Eq. (17)

The constant 8.33 represented the molecular mass ration of carbon to calcium carbonate.

3.5 Quality control - Chauvenet's criterion

For the quality control of the biomass data purposes, the maximum documented pteropod carbon biomass was identified and compared with the carbon biomass values calculated from the abundance measurements (see chapter 4.4 for further explanation).

After calculating biomass values, the Chauvenet's criterion was used to exclude statistical outliers from the gridded pteropod database (Glover et al., 2011). As the total summarised biomass data were not normally distributed, log-transformation (log-normalization) was required (Buitenhuis E.T. et al., 2012a). In this specific case one-sided Chauvenet's criterion was applied to identify only the high value outliers, because the very low and zero biomass values present a true reflection of the ecology in the oceans (Buitenhuis E.A. et al., 2012a). This approach of quality control was done in the MAREDAT datasets of all eleven PFTs, to avoid overrepresentation of high values of biomass (Buitenhuis E.T. et al.., 2012a).

Chauvenet's criterion is a widely accepted statistical method used to identify the data points that can be considered for rejection: it defines an acceptable scatter of values around the mean value of a given sample of N measurements (Kirkup L., 2002).

Chauvenet's criterion assumed that the data is normally distributed (Buitenhuis E.A. et al., 2012a). To test if a particular extreme value is an outlier, one calculates the probability that, given a normal distribution of N measurements with calculated mean value and standard deviation, a randomly selected data point would be at least z=(x-mean)/std away from the mean or farther (Taylor R.J., 1996; Kirkup L., 2002). This probability is multiplied by the total number of data points in the sample and if the resulting product is ≤ 0.5, then the point is identified as an outlier (Kirkup L., 2002). Chauvenet's criterion should be applied only once to a given sample of values – if a certain outlier is rejected and the mean and standard deviation are subsequently recalculated, the criterion should not be applied to the remaining data, because with the newly calculated mean and std, more measurements may be recognised as outliers (Taylor R.J., 1996; Kirkup L., 2002).

4 RESULTS

In this section, the results of pteropod global biomass were presented, with particular focus on pteropod spatial (latitudinal and depth) and temporal (seasonal) distribution, along with carbon budget and productivity estimates. Finally, the data was also critically evaluated.

The final outcome of data mining resulted in two complete pteropod biomass datasets, both publicly available at PANGEA data archive (http://doi.pangaea.de/10.1594/PANGAEA.777384):

1. Raw data file, containing 25 939 datapoints with each point including information on location (longitude, latitude), depth, and time of observation, (day, month, year) pteropod abundance (in units of ind. m^{-3}), calculated pteropod carbon biomass (in units of mg C m^{-3}), mesh sizes, additional information on sampling methodology and a reference (Bednaršek N. et al., 2012c).
2. Gridded biomass dataset (360 x 180° grid, vertical resolution 33 WOA depth levels) converted into NetCDF file format, which is the form to be used for model evaluations. Contained are data on longitude, latitude, sampling depth, month, abundance (in units of ind. m^{-3}) and carbon biomass (in units of mg C m^{-3}) (Bednaršek N. et al., 2012c).

In addition, physiological data on pteropods was gathered and compiled in a dataset found in Annex B. It contains data on respiration rates (in units of g C g C^{-1} day^{-1}), ingestion rates (in units of g C g C^{-1} day^{-1}), gut evacuation rates (in units of h^{-1}), mortality rates (in units of day^{-1} and $year^{-1}$), growth rates (in units of g C day^{-1}) all as a function of temperature, PIC:POC (mol:mol) ratios and finally, the threshold food concentration and food preferences of various species. The physiological data presents a pre-basis for future modelling work.

Further on in this section, the results of pteropod global biomass distribution characteristics, carried out in Matlab are numerically presented in tables and graphically in Matlab generated figures, accompanied by the text descriptions and explanations.

4.1 Pteropod global biomass concentration, distribution and characteristics

Pteropod dataset consisted of 15 134 data points on abundance and biomass, including shelled and non-shelled pteropods, as well as zero and non-zero data entries. Out of 15 134 data entries, 10.6% (1608) were zero values. Out of this, 14 136 data points, which is 93% of all data entries, represented thecosomatous (shelled) pteropods with the rest representing gymnosomatous (non-shelled) pteropods.

The global distribution of sampling stations, where the observations providing pteropod abundance and biomass concentration values were performed, showed that there was a higher frequency of sampling in the NH in comparison with the SH. In the SH, only 23% of (non-zero) data points were recorded, with certain regions being considerably undersampled (Figure 5). In the South Atlantic and South Pacific marine ecoregions, with coastal zone of Temperate South America (Marine Ecoregions Of the World classification according to Spalding M.D. et al., 2007), along with a great part of coastal

zone of Temperate Australasia and in the majority of the Southern Ocean, very little or no abundance or biomass observation studies were conducted (Figure 5). However, some of the areas in the NH were also undersampled, such as the area in the North-Eastern Pacific, the Eastern Arctic regions, as well as the Northern Atlantic, with the tendency of research focusing on the coastal areas – the Temperate Northern Atlantic Zone (MOEW classification according to Spalding M.D. et al., 2007; Figure 5, this study).

All pteropod biomass concentration values gathered within the dataset spanned over four orders of magnitude. The mean biomass concentration calculated for the entire dataset (all pteropods), including zero and non-zero values was 4.09 mg C m^{-3}, with standard deviation (std) of 59.06 and with the median value 0.0083 mg C m^{-3} (Table 3). The mean biomass concentration calculated for non-zero biomass values was 4.58 mg C m^{-3} (std= 62.46), with median value 0.0145 mg C m^{-3}. In the NH, the mean value for non-zero biomass data was 4.04 mg C m^{-3} std= 64.84), and in the SH 8.15 mg C m^{-3} (std= 45.35), which is twice as much as in the NH. However, the median value in the NH was 0.02 mg C m^{-3}, whereas in the SH in was 0.001 mg C m^{-3} (Table 3).

Table 3*: Mean, median, maximum and minimum global pteropod biomass concentrations in mg C m^{-3} including standard deviation (std) values for all data, non-zero data and separately for the Southern and the Northern hemisphere.*

Summed biomass data	**Mean (mg C m^{-3})**	**Std (mg C m^{-3})**	**Median (mg C m^{-3})**	**Max (mg C m^{-3})**	**Min (mg C m^{-3})**
All data	4.09	59.06	0.0083	5.05e+003	
Non-zero data	4.58	62.46	0.0145	5.05e+003	1.00e-006
For the NH non-zero data	4.04	64.84	0.02	5.05e+003	1.00e-006
For the SH non-zero data	8.15	45.36	0.001	608.35	2.00e-006

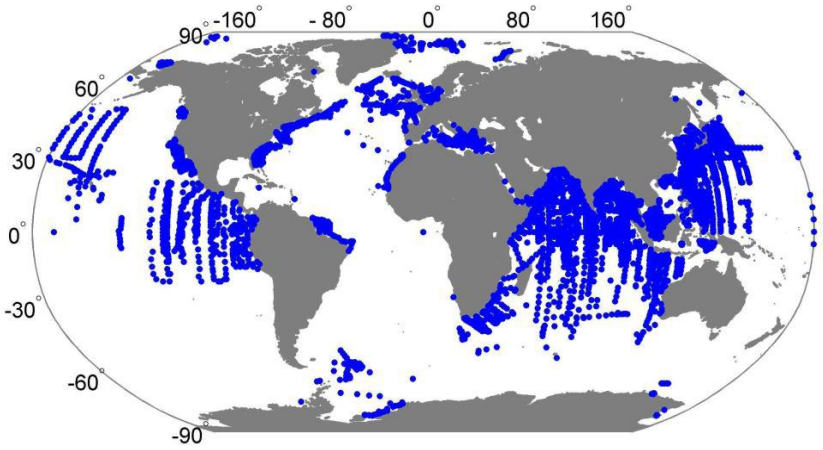

Figure 5*: Global distribution of sampling stations, where quality controlled data on pteropod abundance/biomass was recorded.*

The overall maximum biomass concentrations for both groups of pteropods were estimated from the measurements performed in the temperate region of the NH (Nova Scotia). The maximum estimated biomass of gymnosomes was 5045 mg C m^{-3}, whereas 2979.7 mg C m^{-3} was the maximum estimated biomass of thecosomes (Table 3). The maximum estimated biomass concentration value in the SH was 608.35 mg C m^{-3}, calculated from the measurement performed in South Indonesia (Schnack-Shiel S.B. and Cornils A., 2009) (Table 3). The data source did not specify which group of pteropods contributed to this biomass concentration.

4.2 Pteropod carbon budget and production rates

The value of global mean pteropod biomass concentration (4.58 mg C m^{-3}) was extrapolated over global ocean surface and the depth of 300 m (an estimated depth of pteropod overall occurrence) (Bednaršek N. et al., 2012c). For the global ocean surface value, $322x10^6$ km^2 excluding shelves was taken as a minimum and a total ocean surface of $362.03x10^6$ km^2 as a maxium value (Bednaršek N. et al., 2012c). The resulting pteropod carbon biomass budget ranged from 444 to 505 Tg C at any point of time (Table 4), which is more than two times of annual carbon biomass by diazotrophs, recently estimated to be 50-150 Tg C (geometric mean) (Luo Y.W. et al., 2012) and similar to diatom carbon biomass production estimation of 444-582 Tg C (Leblanc K. et al., 2012). A one-year turnover rate was used for calculating the pteropod production rates from the standing carbon biomass stock (Bednaršek N. et al., 2012c). Therefore, pteropod carbon biomass production rates ranged from 444 to 505 Tg C yr^{-1} (Table 4). The annual carbon production of pteropods is five times bigger than the carbon production of planktic foraminifers of 25-100 Tg C yr^{-1} extrapolated to the global scale, which was recently estimated by Schiebel R. and Movellan A. (2012).

4.3 Global carbon and carbonate biomass characteristics of shelled pteropods

Shelled pteropods (thecosomes) represented the largest share (93%) of data points in the dataset. The mean biomass concentration calculated from non-zero values of the shelled pteropods was 3.81 mg C m^{-3} (std= 40.24) , the maximum biomass concentration 2979.7 mg C m^{-3} (Nova Scotia, NH temperate region; NOAA, 2011) and the median value was 0.0078 mg C m^{-3}. Shelled pteropods therefore account for 83% of the total (mean) global pteropod biomass concentration, with gymnosomes contributing the remaining 17%. This is the first global assessment of the contribution of thecosomes vs. gymnosomes to global pteropod biomass concentration.

The aragonite shell makes thecosomatous pteropods an important player in the biogeochemical carbonate cycle. The mean carbonate biomass of thecosomes (shelled pteropods) was 8.57 mg $CaCO_3$ m^{-3} and the maximum was 6.7 g $CaCO_3$ m^{-3}.

Table 4*: Carbon budget and production of all pteropods, with $CaCO_3$ production of shelled pteropods; extrapolated over min and max global ocean surface area.*

	Mean Carbon biomass of all pteropods (Tg C)	**Carbon production of all pteropods (Tg C yr^{-1})**	**$CaCO_3$ production of shelled pteropods (Tg C yr^{-1})**
Min Area (322.0.3x10^6 km^2)	444	444	828.838
Max Area (362.0x10^6 km^2)	505	505	942.714

From the global carbon production 444 – 505 in Tg carbon per year units, the global $CaCO_3$ production of shelled pteropods per year was calculated, using 8.33 conversion factor (see 3.4 chapter in Methods section). Furthermore, the result of the analyses showing shelled pteropods contributed 83% of the global mean biomass concentration was taken into account and thus only 83% of the global pteropod carbon production was used in conversion to $CaCO_3$ global production. Consequently the annual $CaCO_3$ production of shelled pteropods accounted for 828.838 to 942.714 Tg $CaCO_3$ yr^{-1}. The range of these results is comparable with the global aragonite production (mostly accounted to pteropods) model output of 0.3 Pg C yr^{-1} obtained by Gangstø R. et al. (2008) that considers pteropods represent 35% of total net pelagic carbonate production. The global annual calcification of coccolithopohores estimated by Blach W.M. et al. (2007), 1.6 ±0.3 Pg PIC yr^{-1} is approximately double the annual carbonate production of pteropods estimated in this study. The additional relevant estimations of carbonate/aragonite (global) production and export fluxes done in previous studies are summarized in the Annex C.

4.4 Temporal distribution of data

Collected data were reported from the years 1950 to 2010 (Figure 6), with the lowest numbers of observations in the 1980s and around 2010, while all other time periods

were covered in a more consistent manner, having at least one sampling peak per each decade. The highest number of samples was collected during the mid and late 1960s and by early 1970s. More systematic sampling occurred from the 1990s into 2000 and onwards, while data frequency diminished around 2010 (Figure 6). During 1960-70s and 1990-2000s, the sampling rates were the highest per decades, in both cases reaching 33% share of all the sampling conducted in the period between 1950 and 2010. The largest amount of pteropod abundance measurements was reported in the year 1958.

The level of seasonal bias per both hemispheres was indicated by dividing the data into four seasons. In the NH, the observations were commenced evenly throughout all four seasons: 30% in the winter, 24 % in the spring, 23% in the summer and 24% in the autumn. In the SH, the observations were more often performed in the winter (30%) and summer (25%) and less often in the spring (19%) and fall (16%).

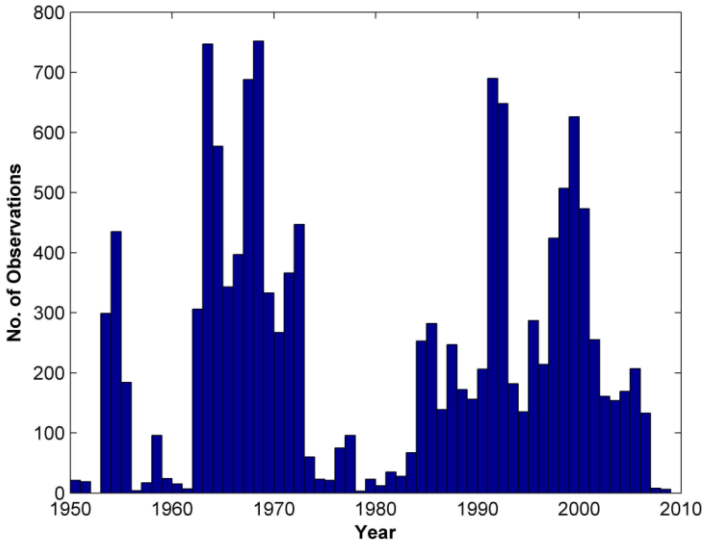

Figure 6*: Number of observations per year, between the years 1951-2010.*

Considering data interpretation, SH vs. NH seasonality has to be taken into account: winter season in the NH represents austral summer season. For both hemispheres, the highest percentage of non-zero data was recorded in the summer. The undersampled months in the NH are May, June, November and December. Similarly, in the SH these are May, June, October and November. However, in the NH this indicates less sampled season during early summer and winter, whereas in the SH, undersampling occurs during the spring and early winter (Table 5).

Table 5: *Monthly distribution of non-zero biomass values for the Northern (NH) and Southern (SH) hemisphere. The entries contain all the biomass non-zero values and the representative percentage (%) of each month, as well as representative percentage (%) of each month in the NH and SH for the non-zero biomass entries.*

Months	Entries	NH season	SH season	% non-zero data	% NH non-zero data	% SH non-zero data
January	1185	winter	summer	8.8	8.4	11.7
February	1457	winter	summer	10.8	9.4	20.7
March	998	spring	autumn	7.1	7.4	6.1
April	1298	spring	autumn	9.4	9.5	9.0
May	876	spring	autumn	6.4	6.9	3.7
June	802	summer	winter	6.0	6.4	4.1
July	1352	summer	winter	9.9	10.4	7.1
August	1790	summer	winter	13.1	13.1	13.8
September	1143	autumn	spring	8.5	8.4	9.0
October	1049	autumn	spring	7.8	8.4	3.7
November	859	autumn	spring	6.4	6.8	3.7
December	806	winter	summer	6.0	5.4	10.2

4.5 Latitudinal biomass distribution

Pteropod samplings were conducted in all ten degree latitudinal belts (except 90 to 80° S which does not incorporate a body of water) and pteropods were observed in all ten degree latitude belts (Table 6, Figure 7). The majority of observations were conducted between 10°- 60° N, with the highest number of observations (2958 entries) at 30°- 40° N (Table 6, Figure 7, Figure 8). As much as 77% of non-zero entries were recorded for the NH and only 23% in the SH (Figures 7 and 8). Very low latitudes (especially between 80° - 40° S) remained consistently undersampled.

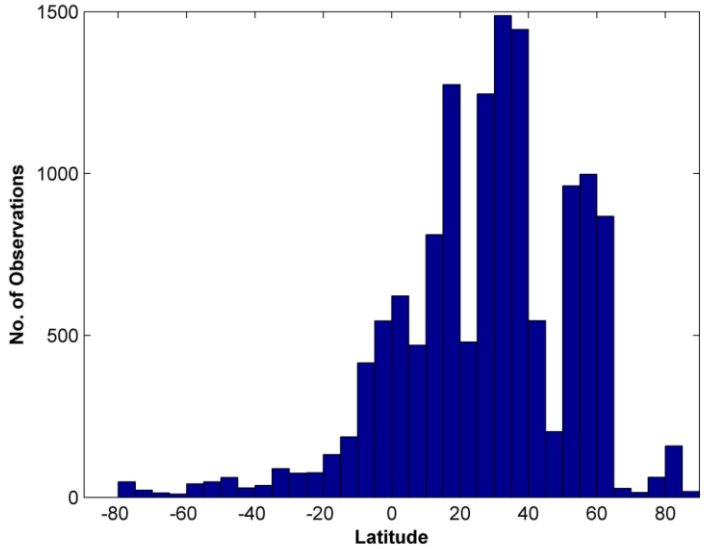

Figure 7*: Number of pteropod observation per latitudinal bands for the period 1951-2010.*

The highest pteropods mean biomass (34.76 mg C m^{-3}) in the NH was recorded in the 40°- 50° N latitude belt (Figure 8). In the same latitudinal belt (42° N, 66° W), the highest maximum (5045 mg C m^{-3}) pteropod biomass was recorded. In the SH, the highest mean (27.2 mg C m^{-3}) and maximum biomass (608.35 mg C m^{-3}) were recorded between 80°-70° S and 10° S - 0° (5° S, 119° E), respectively. Although the overall highest mean and maximum biomass concentrations were recorded in the NH, high biomass values were also measured in different latitude belts and regions throughout ocean basins of both hemispheres.

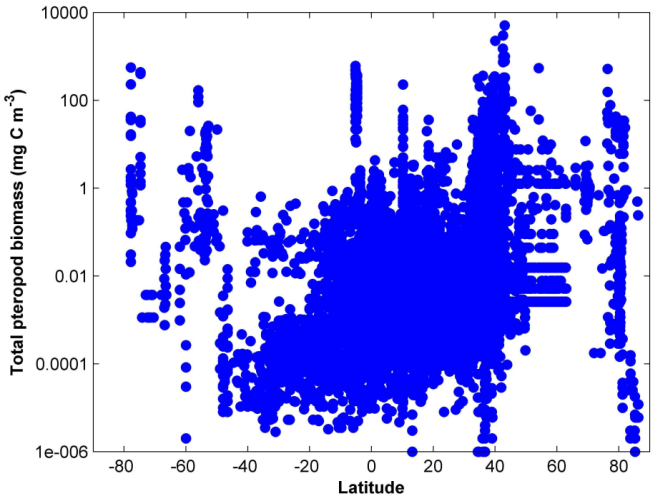

Figure 8: *Distribution of pteropod biomass (mg C m^{-3}) per latitude.*

Table 6: *Latitudinal distribution of pteropod biomass data in ten degree latitudinal belts (90° S to 90° N), where mean, maximum (max), minimum (min), median and standard deviation (std) of biomass per each latitudinal belt were calculated from non-zero entries (from summarized dataset).*

Latitude	Entries	Mean (mg C m^{-3})	Std	Max (mg C m^{-3})	Min (mg C m^{-3})	Median (mg C m^{-3})
90 to 80° S	0	-	-	-	-	-
80 to 70° S	72	27.2	98.44	557.41	0.001	0.19
70 to 60° S	59	0.09	0.42	2.63	2.00e-006	0
60 to 50° S	90	13.93	35.55	168.47	0.01	0.48
50 to 40° S	90	0.25	2.27	21.53	8.00e-006	1.32e-004
40 to 30° S	127	0.02	0.07	0.64	2.83e-006	8.80-005
30 to 20° S	167	0.01	0.05	0.45	5.33e-006	2.18e-004
20 to 10° S	310	0.02	0.08	0.86	3.25e-006	6.14e-004
10° S to 0°	1007	11.93	53.98	608.35	3.50e-006	0
0° to 10° N	1078	0.06	0.26	4.3	4.67e-006	0.01
10° to 20° N	2044	1.47	8.91	226.66	1.00e-006	0.01
30° to 40° N	2958	4.51	21.65	362.89	1.00e-006	0.01

It continues.

Continuing.

Latitude	Entries	Mean (mg C m^{-3})	Std	Max (mg C m^{-3})	Min (mg C m^{-3})	Median (mg C m^{-3})
20° to 30° N	1725	0.06	0.49	9.85	8.00e-006	0.003
30° to 40° N	2958	4.51	21.65	362.89	1.00e-006	0.01
40° to 50° N	744	34.76	248.13	5.05e+003	2.90e-005	0.09
50° to 60° N	1960	1.26	17.26	538	0.003	0.4
60° to 70° N	896	0.31	0.46	11.82	0.003	0.26
70° to 80° N	77	17.31	61.97	517.05	1.75e-004	0.69
80° to 90° N	177	4.6	10.63	34.33	1.00e-006	0.01

The general trend in the SH was a decrease of mean biomass concentrations from the high latitudes towards the Equator. In the NH, mean biomass concentration values were highest in mid-latitudes and decreased towards the North Pole and the equator (Table 6, Figure 7). Notably, in the latitude region between 20° and 30° in the NH and SH, the smallest mean biomass concentrations of each hemisphere were recorded (Table 6). At the poles, similar range of maximum biomass concentrations was recorded, but the mean biomass concentrations (higher near the South Pole – 27.2 mg C m^{-3}) as well as minimum biomass concentrations (lower near the North Pole – 0.000175 mg C m^{-3}) were different (Table 6).

4.6 Depth biomass distribution

The collected field observations reported the occurrence of pteropods in a depth range from the surface (0 m) to the depth of 2000 m. The deepest occurrence was recorded at 2000 m in the Arctic Ocean, for *Limacina* spp. (NOAA, 2012). Global vertical pteropod biomass distribution was spanning over six depth ranges: 0-10 m, 10-25 m, 25-50 m, 50-200 m, 200-500 m and 500-2000 m. Depth distribution, including mean, maximum (max), minimum (min), median and standard deviation (std) per depth range, was calculated from non-zero biomass values (Table 7).

Generally, 83% of all sampling was done in the top 200 m and 62% of all pteropod biomass occurred within this range (Figure 9). This is the reflection of pteropods being predominantly epipelagic, inhabiting the surface layers down to 200 m (Lalli C.M. Gilmer R.W., 1989; Stepien J.C., 1980; Bernard S., 2006). The remaining biomass accounting for 38%, was relatively evenly distributed down to 1000 m, with only a few entries of very low biomass concentration recorded up to 2000 m of depth. The highest number of non-zero pteropod biomass observations was recorded in the 50-200 m depth belt, for which there were 7508 data entries in the dataset (Table 7). However, the highest pteropod biomass concentration values were reported near the surface at the depth range of 0-10, with maximum value of 5045 mg C m^{-3} (at 0 m), mean biomass of 20.65 mg C m^{-3} (std= 157.81) and the median of 0.02 mg C m^{-3} (Table 7).

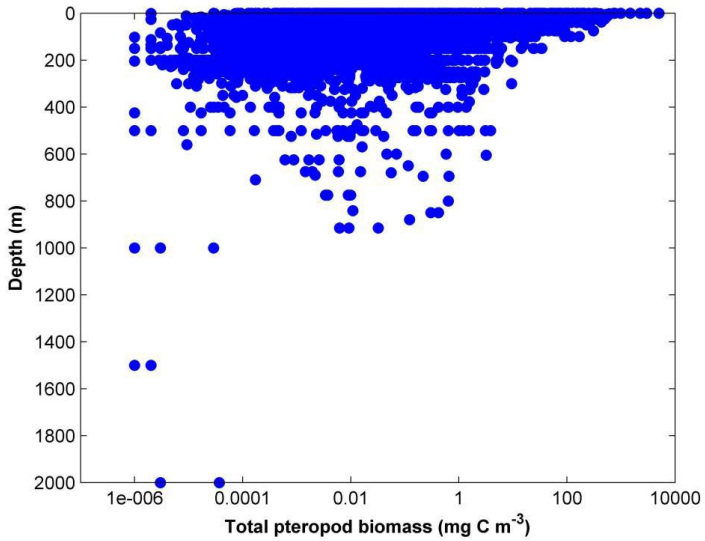

Figure 9: *Distribution of pteropod biomass (mg C m^{-3}) as a function of depth.*

At greater depths, biomass concentrations gradually decreased (Table 7). In four subsequent depth layers to 200 m, concentrations were one order of magnitude smaller from the concentrations in the previous layer. In the last two depth layers (200-500 m and 500-2000 m) the concentrations were two orders of magnitude smaller in comparison with the near surface (10-200 m) depth range (Table 7). In the depth range of 500-2000 m, mean and median biomass concentration values were 0.023 mg C m^{-3} and 0.004 mg C m^{-3} (Table 7), respectively. Carbon biomass concentrations deeper than 500 m were expected to be low, due to the only few known bathypelagic pteropod species (Smith K.L. Jr. and Teal J.M., 1973; Wormuth J.H. 1981, 1985). However, the number of entries between 50-500 m was the highest, indicating that sampling strategies did not impacted biomass distribution results. Depth distribution changed rapidly from the mean surface (0-10 m) concentration of 20.65 mg C m^{-3} to 0.65 mg C m^{-3} in the 50-200 m depth layer. Distinct depth distribution of pteropods is related to the fact that majority of pteropod species inhabit upper 200 m (Stepien J.C., 1980; Lalli C.M. Gilmer R.W., 1989; Andersen V., 1997; Bernard K.S., 2006). Furthermore, the migration of pteropods into surface layers in times of high food abundance (Mileikovsky S.A., 1970; Almogi-Labin A. et al., 1988; Falk-Petersen S. et al., 2008), probably contributed to high carbon biomasses near the surface.

Table 7*: Depth distribution of non-zero biomass values, with mean, maximum (max), minimum (min), median and standard deviation (std) for each depth range. All biomass concentrations are given in mg C m^{-3}.*

Depth range (m)	Entries	Mean (mg C m^{-3})	Max (mg C m^{-3})	Min (mg C m^{-3})	Median (mg C m^{-3})	Std
0-10	1806	20.65	5.45e+003	0	0.02	157.81
10-25	612	14.44	557.41	0	0.038	57.53
25-50	1296	3.25	434.37	0	0.002	18.26
50-200	7508	0.65	308.47	0	0.02	5.74
200-500	2028	0.19	9.85	0	0.002	1.04
500-2000	276	0.023	3.20	0	0.004	0.18

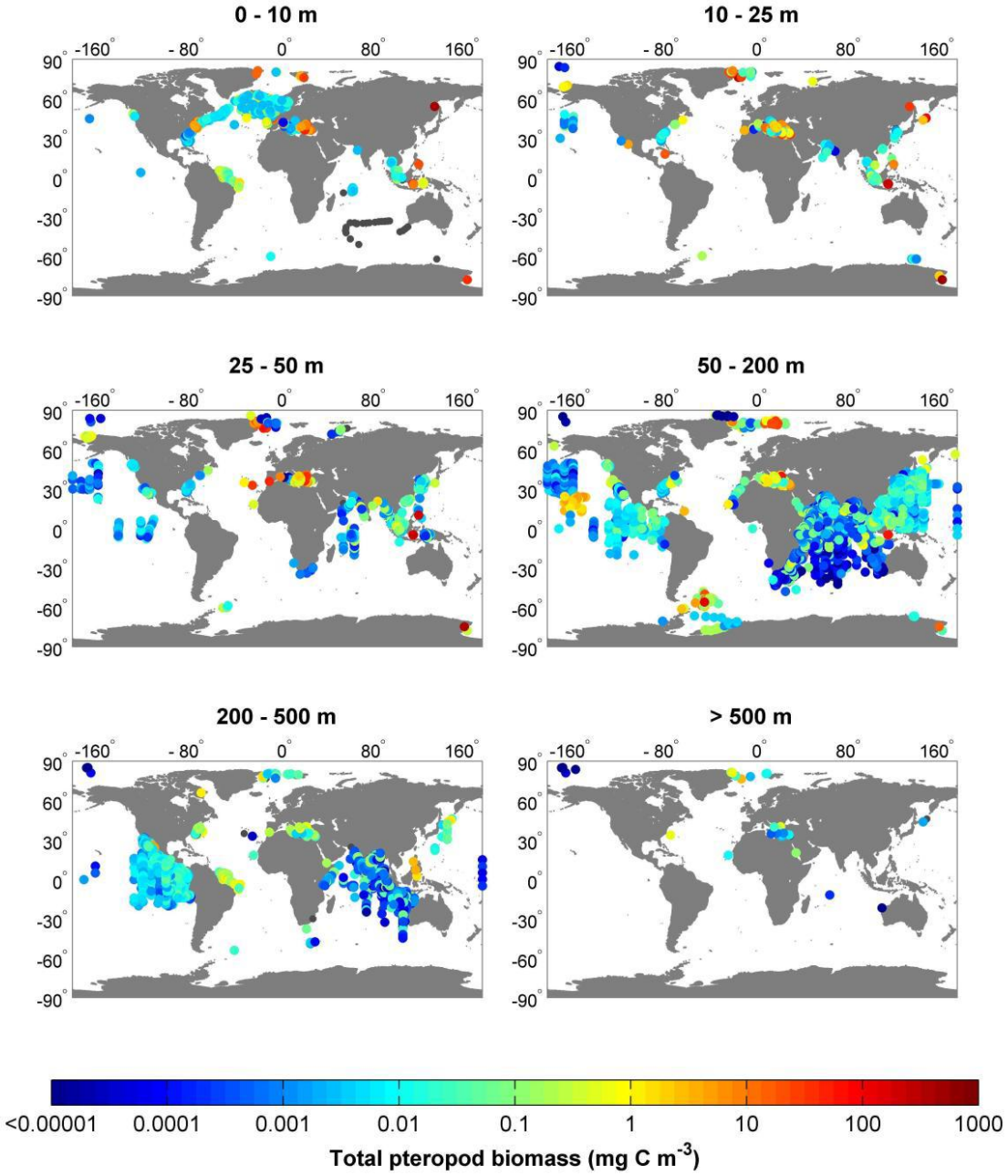

Figure 10: *Recorded pteropod carbon biomass values (mg C m^{-3}) in six depth belts: a) 0-10 m (surface), b) 10-25 m, c) 25- 50 m, d) 50-200 m, e) 200-500 m, f) ≥ 500 m (data from the summarized dataset).*

Pteropod biomass peaks (above 100 mg C m^{-3}) were found between 0-200 m (Table 7, Figure 10). The peaks occurred randomly in different ocean basins, including high-latitudes, temporal and equatorial regions (Figure 10). Within the depth range of 200-500 m, the biomass concentrations declined to 1-10 mg C m^{-3} and the pteropods were mostly observed in equatorial regions. Higher biomass concentration between 200-500 m in the tropical regions indicated, that tropical species, such as *Styliola subula* and *Clio pyramidata* dwell at greater depths than some species living in temperate and

high-latitude regions (Solis N.B. and von Wasterningen H., 1978; Wormuth J.H., 1981; Almogi-Labin A. et al., 1998). Occurrences of some thecosome species (*Cavolinia* spp., *Diacria* spp., *Creseis* spp., *Clio* spp., *Styliola* spp.) were recorded between 800 to 900 m of depth in the Red Sea. The deepest recorded occurrence of an unspecified gymnosome pteropod specimen was also in the Red Sea at the depth of 880 m (NOAA, 2012). However, high-latitude pteropods (e.g. *Clione limacina* inhabiting North Atlantic and subarctic Oceans) are also known to migrate into deeper water layers (500 m) (Mileikowsky S.A., 1970). In the Arctic Ocean, *Limacina* spp. was recorded at 2000 m (NOAA, 2012).

4.8 Seasonal distribution of biomass

In the NH, the highest max biomass concentrations (Table 8) were recorded during the summer (5.05e+003 mg C m^{-3}, August) and spring (3.00e+003 mg C m^{-3}, May). Summer and spring were also the seasons with higher mean biomass concentrations in comparison with the autumn and winter when the mean biomasses declined (Table 8). The mean biomass concentration was highest in spring (5.42 mg C m^{-3}).

***Table 8**: Values for the seasonal distribution of non-zero biomass values in the Northern hemisphere (NH) with calculated mean, standard deviation (std), median, minimum (min) and maximum (max).*

Season	NH mean (mg C m^{-3})	NH std	NH median (mg C m^{-3})	NH min (mg C m^{-3})	NH max (mg C m^{-3})
winter	2.77	15.63	0.016	1 e-006	557.41
spring	5.42	79.94	0.062	1 e-006	3.00e+003
summer	4.32	92.69	0.016	1 e-006	5.05e+003
autumn	2.44	18.39	0.033	1 e-006	765.24

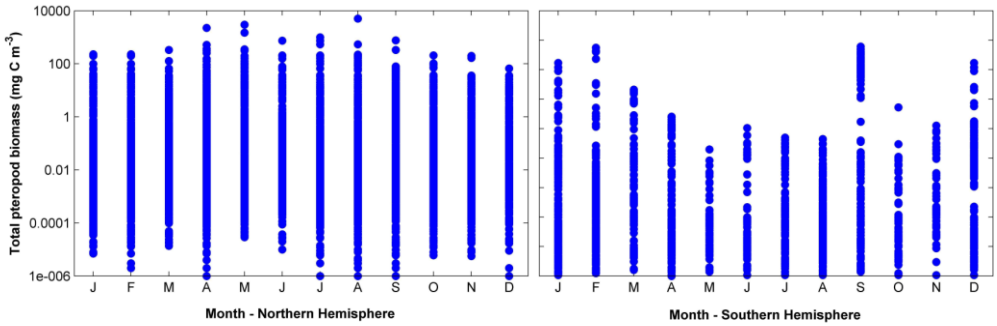

***Figure 11:** Seasonal distribution of pteropod biomass (mg C m^{-3}) in a) the Northern and b) the Southern hemisphere.*

The biomass concentrations recorded in the SH reached the highest value in the spring (608.35 mg C m^{-3}, September) and summer (557.41 mg C m^{-3}, February), but these values were one order of magnitude smaller than the summer-spring biomass peak

recorded in the NH (Tables 8 and 9, Figure 11). The spring mean biomass concentrations (39.71 mg C m^{-3}) were the highest, demonstrating strong seasonal variations in biomass distribution (Table 9). Comparing the seasonal mean biomass fluctuations in both hemispheres, the seasonality in the SH was much greater than in the NH (Tables 8 and 9), which could partially be due to the lack of observational data in the SH.

Table 9: *Values for the seasonal distribution of non-zero biomass values for the Southern hemisphere (SH) with calculated mean, standard deviation (std), median, minimum (min) and maximum (max).*

Season	SH mean (mg C m^{-3})	SH std	SH median (mg C m^{-3})	SH min (mg C m^{-3})	SH max (mg C m^{-3})
winter	0.03	0.09	4.54e-004	2.00e-006	1.06
spring	39.71	93.00	0.009	7.50e-006	608.35
summer	3.73	32.83	0.002	3.00e-006	557.41
autumn	0.51	2.47	7.28e-004	3.30e-006	21.05

4.7 Critical evaluation of data

In the process of obtaining biomass concentrations of pteropods, several different types of errors can be introduced, partly due to sampling methodologies and conversion calculations.

4.7.1 Comparison of recalculated and original biomass values

The majority of data points (89%) out of 25 939 data points collected were pteropod abundance counts and only 11% of the used studies contained pteropod biomass data. The original biomass values provided a threshold for the maximum biomass found in the natural environment of the ocean, which the biomass calculations were compared to with the aim not to overestimate the calculated biomass values. The highest shelled pteropod (*Limacina helicina*) biomass (538 mg C m^{-3}) was recorded in the Sea of Okhotsk (Rogachev K.A. et al., 2008). Compared to this value, the highest calculated biomass value of thecosomes (2979.7 mg C m^{-3}) was one order of magnitude higher. The highest calculated biomass concentration of gymnosomes was 5045 mg C m^{-3} (NOAA, 2011), recorded near the Nova Scotia, the Gulf of Maine (Table 3). The latter was also the highest biomass value in the whole dataset.

4.7.2 Sampling errors and the effect of nets and mesh sizes on global pteropod biomass

The sampling methodologies and equipment (mesh sizes, net types) used during various surveys providing the observational data on pteropod abundance and biomass gathered in the created dataset were different which can result in biased interpretation of the obtained results. Firstly, not only the efficiency of different nets for sampling pteropods of various size classes can differ, but different nets are prone to different

sampling issues, such as net-avoidance behaviour, extrusion of the animals through the mesh and clogging of the net (Harris R.P. et al., 2000). Secondly, the contribution of smaller sized pteropods (e.g. <100 µm) to pteropod populations is often underestimated, due to the insufficient use of the nets with the smaller mesh size (Wells F.E. Jr., 1973). This is of particular problem at certain times/seasons of the year when this size fraction can represent a very large part of the natural populations (Fabry V.J., 1989; Gannefors C. et al., 2005; Tsurumi M. et al., 2005). Furthermore, when small vertical nets are used for sampling, larger size zooplankton can avoid nets, whereas the use of large mesh sizes can miss smaller size population fraction (Boysen-Ennen E., 1991). Consequently, due to the use of specific mesh sizes and diameter of nets, a size selection of species and life stages can be introduced, influencing sampling results, which may consequently result in potentially incorrect conclusions about the densities or composition of zooplankton population under investigation (Wells F.E. Jr., 1973).

In case where size related information of the sampled pteropods was recorded simultaneously with the biomass values and mesh sizes, the impact of mesh sizes on the size range of the captured specimen could be studied. However, as the size data was not available in most studies, this aspect was not analysed.

Where possible, such being the case of 19 671 data points containing information on pteropod abundance/biomass as well as the net mesh sizes used for sampling, an analysis of mesh size influencing the recorded abundance/biomass values was conducted. The results suggested that none of the used nets with mesh sizes between 100-3000 µm were biased toward recording higher abundances and consequently higher biomass concentrations, as the average biomass concentration was similar between different mesh sizes used for sampling (Figure 12). The highest biomass recordings were obtained using 270 µm mesh (Figure 12), which implies that with this mesh size, a size-class of pteropods contributing the most to the biomass concentrations was caught. Therefore, only a few studies, with mesh sizes profoundly bigger than 270 µm, possibly undersampled the important size-class of the pteropod populations and thus biased the estimates of biomass concentrations in this study.

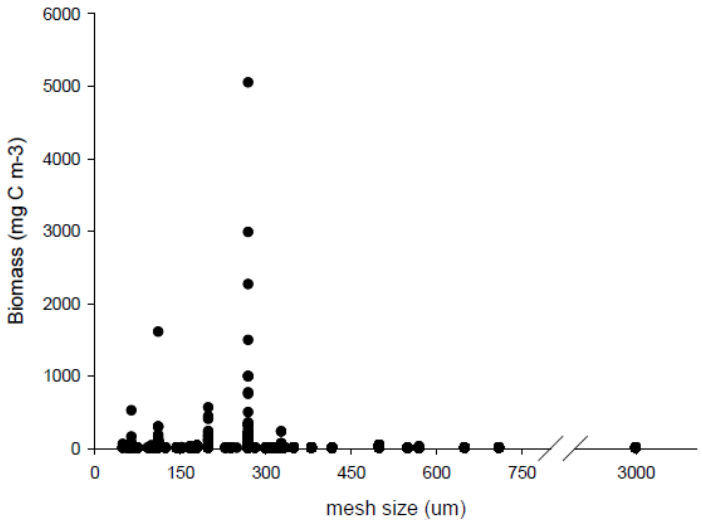

Figure 12: *The effect of mesh size of net used on the biomass calculated in the studies. Zero data were excluded.*

In addition, the analysis of mesh sizes used across different latitudes and longitudes was conducted to examine, whether the use of different mesh sizes at different latitude/longitude followed any specific trend (Figure 13, Figure 14). The results showed that no specific mesh size was used at certain latitude/longitude considerably more often than were the other mesh sizes. As there was no observed geographical trend of mesh size use, this was not considered a source of bias in the large scale geographic analysis of the global pteropod biomass distribution.

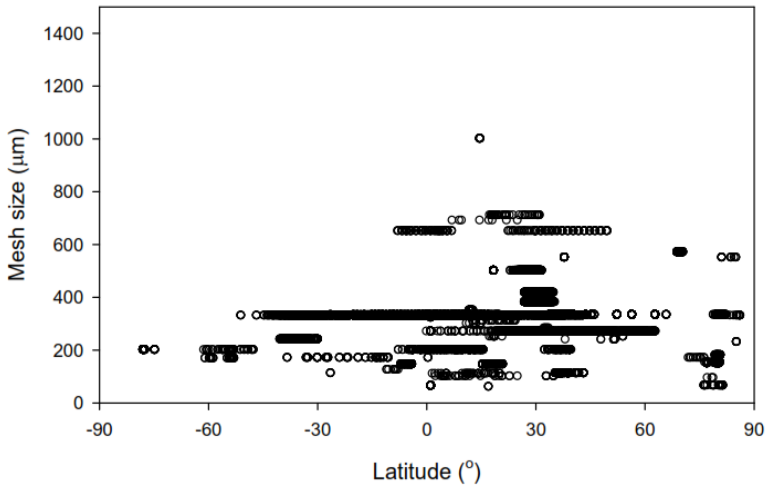

Figure 13: *Mesh size of the net used vs. latitude within dataset. Note: some data were excluded if multiple mesh sizes were reported.*

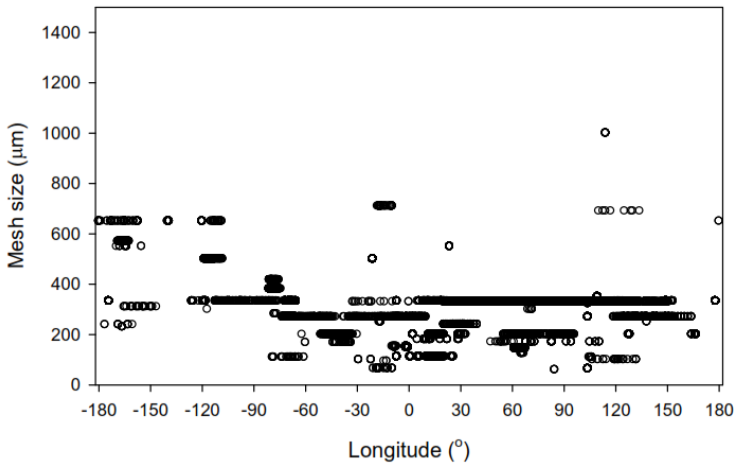

Figure 14*: Mesh size of the net used vs. longitude within dataset. Note: some data were excluded if multiple mesh sizes were reported.*

The results of both analyses indicated that the mesh size was not a source of a large-scale bias. As a result, no data points were eliminated due to the criteria of different sampling strategy (mesh size and net type). However, the comparison of biomass data

obtained with such broad range of different mesh sizes certainly introduces an error of the biomass values in the database, but any elimination of data would ultimately reduce the scope of the database. It is thus of fundamental importance to keep all the information on sampling strategies, mesh sizes and net types collected from literature included along with the database. Accordingly, all the accessible information was included to the data file uploaded on web-archive PANGEA.

4.7.3 Errors related to conversion equations

As the aim of this work was to create a database of global pteropod carbon biomasses, the majority of data collected as abundance measurements had to be converted into biomass values using available conversion equations based on length-to-weight conversion (explained in the Methods section). Potential bias for biomass calculation was introduced when calculating the average lengths for different pteropod species and groups of pteropods (Annex A; explained in the Methods section) as the average size of the animals was not known from datasets. Furthermore, whenever the information about the life stage of the sampled animals was not specified in the data source, the specimens were considered as adults and the average length of the adult stage was used in the length-to-weight conversion. In case, the sampled specimens were not adults (or at least part of the population consisted of juveniles) the result of the calculation could be an overestimation of the biomass.

In addition, a certain level of bias was introduced as not for all the pteropod species, species-specific length-to-weight conversion algorithms existed (explained in the Methods section). For such species, it was necessary to use conversion equations of different species, based on their similar shapes and morphologies. However, in many studies and data sources, the name of species was not provided or specified beyond the name of the group of pteropods recorded (e.g. Pteropoda, Thecosomes, Euthecosomes, Gymnosomes). The error was thus firstly introduced with the use of a more general length-to-weight equation (Davis C.S. and Wiebe P.H., 1985) for these groups of pteropods and secondly, with the use of averaged length for specific group of pteropods (Table 2, Annex A). In this case again, if the sampled specimens were adults, the result of the calculation were possibly underestimated or reversely, if the recorded animals were juveniles, calculated results were possibly an overestimation of carbon biomass.

Further bias stems from the fact that the biomass is a product of abundance and weight, thus the errors of two separated parameters get multiplicated.

To conclude, although some biases could not be avoided in biomass calculations, the comparison of the calculated biomasses versus the field-recorded biomasses are similar, at the most differing by factor five (2979.7 mg C m^{-3} vs. 538 mg C m^{-3}; chapter 4.4). These results demonstrate that calculated biomass values are reliable and accurate, and further validate the methodological approach that was applied for abundance to biomass conversion. The Chauvenet's criterion was applied to discard any statistical outliers among the pteropod biomass values in the database. The critical value (z) for the dataset of all pteropods (gymnosomes and thecosomes) was four times the standard deviation from the average. Using Chauvenet's criterion, no statistical outliers were identified and consequently, none of the biomass values was excluded.

5 DISCUSSION

In the discussion, I tried to portrait the possibilities for pteropod existence in the future, although part of the discussion also focuses on recognising which of the anthropogenically-induced stressors are already in place and therefore having an impact on pteropod population. I also tried to emphasise which of the collected information from this study can be used for predicting the future of pteropods. Although the methodological biases of this study existed and were discussed in the Results section, this discussion assumes that they do not majorly impact the results of the analysis.

I addressed three main stressors driven by the climate change - ocean warming, acidification and deoxygenation by describing each of them in more details and also in regards to the areas where these changes will be most pronounced. The impact of the stressor were evaluated through the gathered data on physiological and behavioural responses of pteropods, further investigating whether any of the predicted impacts of the three stressors can already be identified from the results i.e. current dynamics of pteropods in their environment, obtained with the analysis of the distribution of pteropod biomass data. The accurate understanding of present dynamics could help to predict dynamics of pteropods in the future (Matson P.G. et al., 2011). For this reason, I assessed pteropod vulnerabilities/resiliencies under current environmental factors as they indicate pteropod ability to adapt and survive conditions in the changing marine environment in the future (Hoffman G.E. and Todgham A.E., 2010).

In separate subchapters, I discussed possible synergetic effects of the three stressors on pteropods and the potential implication of the loss of pteropods on ecosystem functioning. Finally, the importance of pteropods as a PFT was highlighted, but also requirements for future research concerning pteropods were taken into consideration.

5.1 Global environmental ocean changes (ocean warming, deoxygenation and acidification)

Ocean acidification, ocean warming and ocean deoxygenation are the three main environmental stressors driven by raising CO_2 levels in the Earth's atmosphere accelerated by harmful human activities, with the potential to affect pteropods (Fabry V.J. et al., 2008; Keeling R.F. et al., 2010; Gruber N., 2011; Seibel B.A., 2011). To predict the impact of these environmental stressors on a diverse group of animals such as pteropods is a complicated task. Firstly, considering pteropods are a very diverse group of molluscs with different adaptations specific for their natural habitats, vertical and geographical distribution, feeding habits, metabolic rates, all of which define their responses under environmental stressors to be stage-specific and species-specific (Byrne M., 2011). Secondly, the most vulnerable are species from stable low- and high-latitude environments and deep water species, which have very low threshold to tolerate changes in their environment such as warming or shallowing of $CaCO_3$ horizons (Byrne M., 2011; Rosenthal J.J.C. et al., 2012). Thirdly, larvae/juvenile life stages seem to be more vulnerable than adult forms (Bednaršek N., 2010; Comeau S. et al., 2010b; Byrne M., 2011; Lischka S. et al., 2011).The most complex issue however concerns the possibility of complex interactive (antagonistic or synergistic) effects of the stressors on marine animals, such as synergistic action of hypercapnia and hypoxia or hypercapnia and warming on physiological responses of different

marine animals (Widdicombe S. and Spicer J.I., 2008; Hoffman G.E. and Todgham A.E., 2010; Pörtner H.-O. 2008, 2010).

5.1.1 Ocean warming

Over the last 40 years, approximately 84% of the heat accumulating in the Earth system was absorbed by the oceans (Levitus S. et al., 2005). Oceans also take up a great part of the extra heat accumulating in the atmosphere due to the enhanced green house effect (IPCC, 2007; Gruber N., 2011). The consequence of that is a general warming of the upper ocean in particular, although there is a high variability in the warming trends across decades (e.g. from positive to zero, negative trends) (Harrison D.E. and Carson M., 2006; Dominigues C.M. et al., 2008), years, seasons and regions (e.g. ocean basins) (Barnett T.P., 2004; Harrison D.E. and Carson M., 2006; IPCC, 2007). In the last 50 years, the temperatures in the 0-700 m depth layer increased by approximately 0.1 °C, whereas the mean near surface ocean temperatures increased by approximately 0.7 °C in the last 100 years (IPCC, 2007). Further physical consequences include melting of the sea ice (Yin J. et al., 2011), changes in salinity (IPCC, 2007), increased upper ocean stratification and changes in the upper water mixing and transport of nutrients/gasses through the water column (Gruber N., 2011).

5.1.1.1 Physiological mechanisms of pteropods behind the expected trends of ocean warming

Direct effects of ocean warming on marine animals, including pteropods, are expected due to the temperature dependent rates of physiological processes and functions, such as enzyme performance, membrane fluidity, energy requirements and primarily the oxygen consumption (Pörtner H.-O. 2008, 2010; Hofmann G.E. and Todgham A.E., 2010; Maas A.E. et al., 2012b; Storey K.B. and Tanino K.K., 2012). Thermal niches are species-specific and define the sensitivities of species to ocean warming (Pörtner H.-O., 2001). The thermal niches can also vary within species due to phenotypic adaptations specific to their living environment (Pörtner H.-O., 2002; Rosenthal J.J.C et al., 2012; Storey K.B. and Tanino K.K., 2012). The limited performance at high temperature outside of the thermal widow is correlated with insufficient oxygen uptake/delivery in comparison with increased oxygen demand of animals (Pörtner H.-O., 2001). Elevated temperature may thus enhance growth, development and calcification of animals, but only until the animals reach their thermal limit (Byrne M., 2011). Long-term exposure to extreme temperatures and thus long lasting reduced oxygen supply may detrimentally affect the fitness of the animals, consequently influencing their activity, growth and reproduction (Hofmann G.E. and Todgham A.E., 2010; Storey K.B. and Tanino K.K., 2012). The long lasting changes in habitat temperature may result either in thermal acclimation (a limited shift of optimal performance), evolutionary adaptation (shift of the whole thermal niche) or in the enhanced risk of local extinction and the change in the geographical distribution of the species (Pörtner H.-O. 2008, 2010; Hofmann G.E. and Todgham A.E., 2010). Many marine animal species, among those also 24 zooplankton species, have recently showed an altered geographical distribution, such as the ranges of species expanding poleward due to the warming of the oceans (Parmesan C. and Yohe G., 2003). Similar trend of poleward migration might be expected from pteropods, this affecting their global distribution (Comeau S. et al., 2011).

Another physiological response of pteropods to ocean warming be initiated via changes in the quality (Perissinotto R., 1992; Bernard K.S., 2006; Maas A.E. et al., 2011) and quantity as well as timing of their food (Seibel B.A. and Dierssen H.M., 2003; Bernard K.S., 2006). Therefore, thecosome pteropods could be indirectly impacted by the physical changes in the environment due to global ocean warming (and change in radiation), through the changes in the quality and quantity of phytoplankton, which presents one of their main food sources (Torrtell et al., 2008; Seibel B.A. et al., 2012). Warmer temperatures increase energy demands of animals, resulting in higher metabolic rates and consequentially increased demand for food (Christou E.D. and Moraitou-Apostolopoulou M., 1995; Seibel B. et al., 2007; Comeau S. et al., 2010a; Mass et al., 2012b). Thereby, wintertime rise in temperatures due to ocean warming may result in higher metabolic rates of the overwintering pteropod specimen (Smith K.L. Jr. and Teal J.M., 1973; Seibel B.A. et al., 2007; Comeau S. et al., 2010a; Maas et al., 2012b), consequently increasing their food demands at times when food will not necessarily be available. The correct timing of food availability, especially phytoplankton blooms, is crucial for stability of pteropod populations (Seibel B.A. and Dierssen H.M., 2003). Food deprivation can result in depressed metabolic rates, consequently suppressing costly process like reproduction, resulting in delayed spawning and slowing down of development and metamorphosis (Seibel B.A. and Dierssen H.M., 2003; Bernard K.S., 2006; Böer M. et al., 2006; Bernard K.S. and Froneman P.W., 2009). In the seasonal or short-term events of unfavourable food conditions, population can recover, whereas long-term unfavourable conditions might cause local disappearance of pteropod population (Seibel B.A. and Dierssen H.M., 2003). This is especially important in the light of the high-latitude species, where the reproduction does not stop during the winter time (Bednaršek et al., 2012a). The responses on phytoplankton structure shifts could be species-specific, as different pteropod species have different food preferences. As the thecosomatous pteropods were mostly observed to be highly opportunistic omnivores, adapted to switching between different food sources depending on the availability (Wormuth J.H., 1985; Perissinotto R., 1992; Gilmer R.W. and Harbison G.R, 1991; Gannefors C. et al., 2005), they might thus be in advantageous position in the environment with variable and changing food quality and abundance. Additionally, as the gradual shifts towards smaller primary producers (pycoplankton) are predicted to take place in the warming ocean (Moran X.A.G. et al., 2010), this could have a positive impact on certain pteropod species, such as *Limacina* spp*.,* which preferentially grazes on pico- (<2 μm) and nano-plankton (Perissinotto R., 1992; Bernard K.S., 2006). On the other hand, the warming environment may be the cause for a decrease in the mean and maximum sizes of pteropods themselves, which is a trend of adaptation to changed environment generally expected among the marine ectotherms, as there will be higher costs of thermal stress mitigation and thus less energy will be invested into the growth of animals (Daufresne M. et al., 2009; Storey K.B. and Tanino K.K., 2012). Within pteropod group, sizes decreasing in regions with higher temperatures were documented for some species (Van der Spoel S., 1970; Lebour M.W. 1931 cited in Böer M. et al., 2005).

5.1.1.2 Predictions for specific areas

The heating of the world oceans is not uniform and is regionally penetrating to different depths due to various reasons, such as the natural variabilities in the advection of heat by ocean currents in different ocean basins and differences in aerosol concentration in the atmosphere over the oceans (e.g. NH enters more CO_2 into the atmosphere than SH) affecting regional warming rates (Barnett T.P. et al., 2005; Levitus S. et al., 2005).

The CO_2-induced warming is thus penetrating deeper in the North Atlantic than in the North Pacific, Indian and the Southern Ocean (Barnett T.P. et al., 2005; IPCC, 2007). The estimations of ocean warming also differ as a result of different assessment methods (Lyman J.M. et al., 2010).

Global mean surface ocean temperatures are projected to rise for 0.94 °C to 1.97 °C by the end of the 21st century, under the IPCC SRES B1 and A2 emission scenarios, respectively (Steinacher M. et al., 2009). The warming is predicted to be the strongest in tropics and higher latitudes of NH (Gruber N., 2011). Only a 0.3 °C temperature rise (under A2 scenario) is expected to occur in the surface layers of the Arctic Ocean (Steinacher M., 2009). However, certain model predictions for the 21st century (under IPCC SRES A1B scenario) show a pronounced warming (2.0 ±1.1 °C) in the subsurface layers (200-500 m) in the North Atlantic, around Greenland (Yin J. et al., 2011). Conversely, the subsurface warming in the Southern Ocean around Antarctica is projected to be only 0.6 ±0.4 °C, due to the deep currents presenting a strong barrier, protecting the Southern Ocean against poleward heat transport and consequently also resulting in mainly unchanged ice conditions in Antarctica (Yin J. et al., 2011; Gruber N., 2011). In the last 50 years, the freshening of the water due to sea ice melting and increased precipitation with consequential drop in salinity was nevertheless most pronounced in the upper 500 m of the polar regions of both hemispheres (north of 50° N and south of 70° S), whereas in subtropical regions the salinity increased (IPCC, 2007). The changes in salinity (upper water freshening) and water temperature are expected to be the cause of increased ocean stratification (IPCC, 2007; Yin J. et al., 2011; Gruber N., 2011).

Enhanced surface ocean stratification will result in reduced transport of nutrients and gasses by vertical mixing in the water column (IPCC, 2007; Gruber N., 2011), which will also have an impact on primary production (Behrenfeld M.J. et al., 2006; Martinez E. et al., 2009; Boyce D.G. and Lewis M.R., 2010). The strongest stratification is expected to occur in tropics, due to increased precipitation and in the Arctic Ocean, due to freshwater input as a result of sea ice melting and increased precipitation (IPCC, 2007; Steinacher M. et al., 2009; Gruber N., 2011). However, the strongest effect of enhanced stratification of the surface ocean on phytoplankton growth, i.e. a reduction in productivity, is predicted to occur in low- and mid-latitudinal areas, where nutrients are naturally limited in the upper layers (Behrenfeld M.J. et al., 2006; Martinez E. et al., 2009; Boyce D.G. and Lewis M.R., 2010). On the contrary, in the cooler regions of higher latitudes, where the turbulences are stronger and nutrients available, the warming and stratification are expected to lead to increase in phytoplankton abundances (Richardson A.J. and Shoeman D.S., 2004). The primary production in high latitudes may be additionally stimulated by the increased availability of photosynthetic active radiation, penetrating into the ocean due to the disappearance of the sea ice cover (Steinacher M. et al., 2009).

Moreover, phytoplankton community structure shifts from larger to smaller cell sizes have been proposed as a direct response to the rising temperature (Moran X.A.G. et al., 2010) and as indirect consequences of nutrient shortages (caused by enhanced stratification, especially in the open ocean) and temperature-mediated changes in grazing pressures (in eutrophic areas) (Marañón E. et al., 2012; Chen B. et al., 2012). However, trying to anticipate a universal effect of ocean warming on phytoplankton size structure is risky since the relationship between temperature and resources supply is spatially and temporally highly variable (Marañón E. et al., 2012). Therefore the changes in distribution and structure of phytoplankton due to global ocean warming remain uncertain, as multiple studies provide different scenarios (e.g. Richardson A.J.

and Schoeman D.S., 2004; Boyce D.G. and Lewis M.R., 2010; Marañón E. et al., 2012; Chen B. et al., 2012). Nevertheless, the common assumption is that the potential impacts on phytoplankton will strongly differ on spatial and temporal scales (Martinez E. et al., 2009; Boyce D.G. and Lewis M.R., 2010).

5.1.1.3 Comparison of predicted trends and current observations

The correlation between the food abundance and pteropod abundances in the dataset analysis might be drawn in the case of seasonal pteropod carbon biomass fluctuation. The biomass concentrations in both hemispheres reach the highest mean values in spring, with the lowest concentrations in winter. These abundance fluctuations are in accordance with observations of pteropod life cycles, in majority exhibiting intensive reproduction (spawning) and growth in spring and summer due to the high food abundance (Bernard K.S., 2006; Böer M. et al., 2006; Hunt B.P.V. et al., 2008; Bernard K.S. and Froneman P.W., 2009), especially in high-latitude regions where there is a pronounced seasonality in food abundance due to extreme abiotic environmental conditions favouring short-term intensive primary production in spring/summer season (Kobayashi H.A., 1974; Lalli C.M. and Gilmer R.W., 1989; Böer M. et al., 2005; Gannefors C. et al., 2005; Bernard K.S., 2006; Bednaršek N. et al., 2012a). Additionally, the correlation of high pteropod abundances with the availability of their food source was also confirmed in the results of the pteropod biomass depth distribution (Bednaršek N. et al., 2012c). The highest mean and max pteropod carbon biomass concentrations were recorded in the upper 200 m of the water column as the majority of pteropods inhabit the near surface waters down to 200 m (Lalli and Gilmer, 1989; Stepien J.C., 1980; Andersen V., 1997; Bernard K.S., 2006), indicating the correlation between high pteropod biomasses and high primary production in the euphotic zone (Seibel B.A. and Dierssen H.M., 2003; Bernard K.S., 2006). Furthermore, higher pteropod abundances were recorded in the areas of higher nutrient loads and productivity, such as the eastern North Pacific (Bednaršek N. et al., 2012c). Based on these correlations, I hypothesise that a strong impact of primary production regime changes on pteropods can be expected.

Change in pteropod distribution due to the ocean warming has not yet been documented and is also not possible to asses from the results of the data analysis in this study. However, vertical and latitudinal shifts in pteropod distributions to avoid stress of the warming environment, such as with many other marine animals (Parmesan C. and Yohe G., 2003), may occur. Pole-ward migrations would be expected especially from the tropical regions and from the North Atlantic or NH in general, where the CO_2-induced warming is projected to be the strongest and penetrate deeper than in the other areas (IPCC, 2007; Gruber N., 2011). High-latitude pteropod species might be especially vulnerable, as they adapted to the life in extremely cold environments with adjustments in their physiology, leaving them with a reduced ability to acclimate to changed environmental conditions (Pörtner H.-O. et al., 2007; Rosenthal J.J.C. et al., 2012). In addition to narrow thermal windows of high-latitude stenotherms, i.e. animals with very narrow thermal window (Pörtner H.-O. 2001, 2002; Pörtner H.-O. et al., 2007), these animals will also be inevitably faced with the smallest available spatial migration scope, considering they already live in the coldest ocean regions and will thus not be able to migrate to sufficiently colder environments in case their natural environment will start to warm up, as such an environment will not exist. Moreover, other obstacles, such as ocean acidification are expected to additionally limit the migration of pteropods as a response to warming of their natural habitats. If pteropods will be unable to either adapt or migrate to less

stressful environment, the extinction of particularly high-latitude, cold water species is expected to occur (Byrne M., 2011; Comeau S. et al., 2011; Bednaršek et al., 2012b).

5.1.2 Ocean deoxygenation

Deoxygenation of the ocean interior is the expected consequence of global ocean warming, directly via the air-sea exchange of oxygen as it is less soluble in warmer water and indirectly due to the enhanced stratification of the upper ocean (preventing mixing of oxygen into ocean interior) and the changed rates of biological oxygen consumption (Keeling R.F. et al., 2010). At the surface, oxygen is in majority utilized by phytoplankton through photosynthesis, whereas in subsurface layers the main oxygen consumers are bacteria decomposing organic particles sinking downward from the sunlit surface layers (Keeling R.F. et al., 2010). The increased upper ocean stratification has the potential of increasing primary production in the surface layers, resulting in increased oxygen demand in deeper layers due to higher downward carbon flux, where at the same time a lower oxygen supply due to decreased mixing with oxygenated surface water will occur (Keeling R.F. et al., 2010).

According to multiple model studies, the global oxygen concentration (~178 μmol L^{-1}) could decline from 1-7% in the next 100 years (summarized in Keeling R.F. et al., 2010). The oxygen minimum zones (OMZs) are expected to expand and thereby hypoxia horizons to shoal (Keeling R.F. et al., 2010). OMZs are defined as the zones of the lowest O_2 concentration in the water column of a certain area and not by the exact O_2 concentration level (Seibel B.A., 2011). OMZs may or may not present hypoxic environment for marine organisms (Seibel B.A., 2011). Hypoxic environment is stressful for aerobic marine organisms (including pteropods), but the thresholds for experiencing hypoxic stress and the ability to survive hypoxia vary greatly between different marine taxa (Keeling R.F. et al., 2010; Seibel B.A., 2011; Maas A.E. et al., 2012b). In addition, in the OMZs the CO_2 levels can reach high concentrations resulting in lower pH and decreased aragonite saturation state (Fabry V.J. et al., 2008; Maas A.E. et al., 2012a).

The changes of oxygen concentrations in the oceans have the potential to affect distribution, abundance, performance and survival of marine organisms (Seibel B.A. and Dierssen H.M., 2009).

5.1.2.1 Physiological mechanisms of pteropods behind the expected trends of deoxygenation

The threshold levels for hypoxia are species-specific (Seibel B.A., 2011), which was observed also among pteropods (Maas A.E. et al., 2012b). The response depends on particular physiological requirements of the species and the O_2 concentrations to which the species is naturally adapted (Seibel B.A., 2011). Taking this into account, the hypoxic conditions, as already mentioned before, should be defined according to species-specific response to low oxygen levels rather than by a uniform oxygen concentration (Seibel B.A., 2011). Similarly, future changes in hypoxic conditions may result in different reactions within pteropod group, due to their species-specific metabolic rates, physiological adaptation, size, life stage and distribution (Maas A.E. et al., 2012b).

The currently existing evidence suggest certain pteropod species (*Hyalocylis striata, Cavolinia logirostros*, C*reseis virgula)* living in habitats of ETP where they daily migrate through O_2 depleted zones (<30 µmol) are adjusted to surviving short-term hypoxia by suppressing their respiration rates for 30-50% or even 80-90% when combined with low temperatures (Maas A.E. et al., 2012b). Other epipelagic pteropod species of the ETP (*Diacria quadridentata, Cavolinia uncinata, Cavolinia inflexa)* on the other hand, have a much lower natural threshold for hypoxia, which is evident from their distribution i.e. exclusion from OMZs (Maas A.E. et al., 2012b). A general response of marine organisms to the shoaling of hypoxia horizons is expected to be migration into shallower, more oxygenated depths (Seibel B.A., 2011). Furthermore, epipelagic pteropod species are expected to be more affected and will change their vertical but possibly also geographical distribution pattern to avoid physiological stress in expanding OMZs (Seibel B.A., 2011; Maas A.E. et al., 2012b). The interactions between predators and the prey could change with the altered daily migration range (Seibel B.A., 2011). Species used to migrating through OMZs are expected to be less affected by the expanding hypoxic environment, but will still have to return to the surface waters with higher O_2 concentrations, to recover from metabolic suppression, to be able to continue to actively reproduce, feed and grow (Seibel B.A., 2011; Maas A.E. et al., 2012b). Therefore, if the depth of well oxygenated layer will shoal, these pteropods will also be forced to change their migration range accordingly (Seibel B.A., 2011). Together with other pteropod species migrating through OMZs, *Creseis virgula* might thus be forced to keep returning to increasingly shallower depths to reach oxygenated water to recover from the metabolic suppression they experience OMZs (Seibel B.A., 2011; Maas A.E. et al., 2012b). However, *Creseis virgula* being a temperature sensitive species might experience high energetic stress in the warming surface waters, which may impose an increased oxygen demand (Maas A.E. et al., 2012b). Oxygen demands of marine organisms are therefore expected to grow due to continuous warming of the oceans (Pörtner H.-O., 2008; Comeau S. et al., 2010a), when simultaneously the supply of oxygen in oceans due to warming will decline (Stramma L. et al., 2008; Gruber N., 2011) and the higher temperatures might further lower the ability of marine organisms to endure hypoxic conditions (Pörtner H.-O. 2008, 2010; Maas A.E. et al., 2012b). In the OMZs of the ETP, additional stress factors beside hypoxia are increased concentrations of CO_2, which can reach >1000 ppm, lowering pH and resulting in aragonite undersaturation (at the depth of 200 m) (Feely R.A. et al., 2004, Fabry V.J. et al. 2008; Maas A.E. et al., 2012a).

5.1.2.2 Predictions for specific areas

OMZs usually occur at depths between 400-1200 m near the base of permanent thermocline, typically in the regions with slow water circulation and poor ventilation (Karstensen J. et al., 2008). In the eastern tropical Atlantic and Pacific Ocean OMZs exist within cyclonic gyres north and south of the Equator (Keeling R.F. et al., 2010). The OMZs at mid-depths also expand over wide areas of North Pacific, in smaller regions of South Pacific and North Indian Ocean, whereas the circulation and ventilation of thermocline waters in SH is much more efficient (Sarmiento J.L. et al., 2004; Karstensen J. et al., 2008). OMZs often occur where there is intensive primary production at the surface with consequent subsurface remineralisation and extensive organic carbon flux to depth, where O_2 utilisation by organisms consuming this organic matter is faster than the ventilation rates supplying O_2 (Karstensen J. et al., 2008). In coastal waters and estuaries, OMZs are frequently a consequence of anthropogenic input of nutrients (Keeling R.F. et al., 2010).

In the last 50 years, a significant decline in oxygen concentrations has already been observed in the subpolar North Pacific and the OMZs of tropical oceans (Ono T. et al., 2001; Whitney F.A. et al., 2007; Stramma L. et al., 2008). Several models predict further decreasing of O_2 levels in the deep North Atlantic, subarctic North Pacific between 200-400 m (Plattner G.K. et al., 2001; Frölicher T.L. et al., 2009) and in the Southern Ocean around 60° S at 200-400 m due to reduced Antarctic convection (Matear R.J. et al., 2000; Plattner G.K. et al., 2001; Matear R.J. and Hirst A.C., 2003; Frölicher T.L. et al., 2009). Modelling studies do not agree in their estimations for tropical regions, predicting both an increase and a decrease of oxygen concentrations, but do majority concur in predicting only small-scale changes (Keeling R.F. et al., 2010).

5.1.2.3 Comparison of predicted trends and current observations

The tropical gyres of the ETP present a natural laboratory in regards to hypoxic conditions, where potentially hypoxic conditions (60 µmol O_2 m^{-3}) on average occur at less than 200 m of depth, occasionally even at 50-100 m (Keeling R.F. et al., 2010). In our just recently published paper (Bednaršek et al., 2012c) it was demonstrated that the highest number of (non-zero) biomass measurements and highest biomass concentrations of pteropods in the tropical areas in Pacific Ocean were recorded at 50-500 m depth, whereby above 25 m and below 500 m the values were substantially smaller. Therefore, the habitats of at least a certain number of tropical species of pteropods could be overlapping with low oxygen areas in the ETP. These would probably be the species, which were observed to be well-adjusted to being regularly exposed to short-term hypoxic conditions, due to their diel vertical migration into tropical OMZs, such as *Hyalocylis striata, Cavolinia logirostris* and C*reseis virgula* (Maas A.E. et al., 2012b).

Similarly, in the Indian Ocean high number of pteropod occurrences (between 50-500 m) overlap with low oxygen zones, as the oxygen concentrations reach 60 µmol O_2 m^{-3} at the depth of 100-600 m (Keeling R.F. et al., 2010). This could indicate again that certain pteropod species are possibly adapted to endure at least short-time exposure to hypoxia. Consequently, the tropical pteropod species with this ability might be less vulnerable to small changes in oxygen concentrations predicted for the tropical areas (Keeling R.F. et al., 2010; Maas A.E. et al., 2012b).

Conversely, expanding deoxygenation in the North Pacific Ocean in the future might affect pteropods differently, because according to the results of the data analysis (Bednaršek N. et al., 2012c), they may not be adapted to low oxygen concentrations. In the North Pacific Ocean, the highest numbers of pteropod biomass measurements and biomass concentrations were recorded between 50-200 m, whereas the potentially hypoxic oxygen concentrations (60 µmol O_2 L^{-1}) mostly occur between 400-800 m (Keeling R.F. et al., 2010). This depth distribution could point to high-latitude pteropod species avoiding and not daily migrating through OMZs. Therefore, these pteropod species may be more sensitive to hypoxia, as they are not regularly experiencing low oxygen concentrations in the range of their natural habitat (Byrne M., 2011; Seibel B.A., 2011; Maas A.E. et al., 2012b). Consequently, they are potentially more vulnerable when the oxygen concentrations continue to decrease in the subarctic Pacific between 400 - 200 m, as predicted (Plattner G.K. et al., 2001; Frölicher T.L. et al., 2009). In case hypoxia horizons will be shoaling into daily habitation zones of pteropods in the North Pacific, vertical distributions of pteropods might change accordingly, with pteropods migrating to shallower depths to avoid hypoxia.

Furthermore, as described before, the hypoxia tolerance is closely interconnected with the thermal window of the animal and the ambient temperature (Pörtner H.-O. 2001, 2008, 2010), which means a species-specific response of pteropods to expanding hypoxia would be also influenced by the extent of ocean warming in the North Pacific and other regions accordingly.

Due to insufficient amount of pteropod biomass data from eastern tropical Atlantic OMZs similar assessment was not feasible for pteropod behaviour in the Atlantic and Pacific tropical OMZs.

5.1.3 Ocean acidification

The world oceans are taking up considerable amounts of CO_2 humans are emitting into the atmosphere, approximately a third of total anthropogenic CO_2 emissions since industrial revolution (Sabine C.L. et al., 2004; Sabine C.L. and Feely R.A., 2007; Khatiwala S. et al., 2009), which is resulting in gradual ocean acidification (Rivkin R.B. and Legendre L., 2002; Sabine C.L. et al., 2004; Raven J. et al., 2005). The expected consequences of ocean acidification are decreasing pH levels and carbonate ion concentrations (Feely R.A. et al., 2004; Orr C.J. et al., 2005; Fabry V.J. et al., 2008; Widdicombe S. and Spicer J.I., 2008). The aragonite saturation is expected to decrease at the surface, as well as in the deep ocean (Steinacher M. et al., 2009). Aragonite undersaturation is also associated with increased freshwater input due to melting of the sea ice (e.g. in the Arctic) and increased precipitation, with consequential decrease in total alkalinity (Steinacher M. et al., 2009; Yamamoto-Kawai M., 2009). As a consequence, this will have large implications for marine ecosystems with particularly great impact on calcifying organisms, including pteropods (Orr C.J. et al., 2005; Fabry V.J. et al., 2008; Gruber N., 2011).

5.1.3.1 Physiological mechanisms behind the expected trends of ocean acidification

Aragonite undersaturation will directly affect shelled pteropods, resulting in the shell dissolution and reduced calcification, thus compromising their survival (Orr C.J. et al., 2005; Fabry V.J. et al., 2008; Comeau S. et al., 2011; Lischka S. et al., 2011; Bednaršek N. et al., 2012b). Furthermore, response of pteropods to elevated pCO_2 is depressed metabolic rate (Maas A.E. et al., 2012a; Seibel B.A. et al., 2012). Reduced metabolism lowers energy demand of the animal, by minimising or delaying energetically costly behaviours and processes, such as high locomotive activity, growth and reproduction until the environmental conditions are less stressful (Guppy M. and Withers P., 1999; Seibel B.A. et al., 2012; Maas A.E. et al., 2012b). However, the usefulness of metabolic suppression as a response to stress is dependend upon the duration and magnitude of the stressor and the adequacy of energy reserves (Maas A.E. et al., 2011). A chronic metabolic suppression coupled with shell dissolution may result in negative consequences for the stability of pteropod population, due to the lack of energy invested in reproduction, development and growth as well as the compromised fitness of pteropods (Guppy M. and Withers P., 1999; Seibel B.A. et al., 2012; Byrne M., 2011; Maas A.E. et al., 2012a). Particularly high deleterious effects in experimental conditions with high pCO_2/low pH were recorded for calcifying pteropod larvae and juveniles, which reflected in malformations of the shells, reduction in shell growth and sizes or even a complete absence of the shells (Comeau S. et al., 2010b; Bednaršek N., 2010.; Lischka S. et al., 2011).

By acclimatization, animals are able to temporarily tolerate stressful environmental conditions, such as the effects of acidification (Pörtner H.-O. 2008, 2010; Byrne M., 2011). As mentioned, the pteropods migrating through OMZs in the tropical Pacific, are also exposed to high pCO_2 and low pH levels (Maas A.E. et al., 2012a). The physical adaptation of species to exposure to higher ambient CO_2 concentrations while migrating into OMZs, may define their sensitivity to increasing CO_2 levels in the future, enabling them to more successfully acclimatize to changed conditions also outside of OMZs (Pörtner H.-O., 2008). However, experiencing hypercapnia independently of deep and cold conditions in OMZs, such as in near surface warming environment, may on the other hand result in different, unpredictable physiological responses of pteropods (Maas A.E. et al., 2012a).

Of higher importance however, are the possible responses of shelled pteropod species to long-term effects of ocean acidification, which will truly define the outcome for their populations:

1. Genetic and physiological adaptation

   Adaptive phenotypic or genetic change is an option for the survival of pteropods in the changed environment (Fabry V.J. et al., 2008; Pörtner H.-O. 2008, 2010; Byrne M., 2011). A change in their life cycle patterns, achieving faster growth and maturation process, increasing the rate of their shell disposition, counteracting dissolution by repair calcification or changing the mineral polymorphism in the shell to counter the shell dissolution (Bednaršek N., 2010; Lischka S. et al., 2011) are some of the possible adaptations.

   The problem with evolutionary adaptation scenarios however, is the time needed for their achievement. If the polar and subpolar areas became undersaturated with aragonite until 2100 (Orr C.J. et al., 2005), pteropods in these regions would only have 50-150 generations to adapt to corrosive conditions, considering one or two generations per year (Kobayashi H.A., 1974; Bathmann U.V. et al., 1991; Bednaršek N. et al., 2012a). It is unlikely, that adaptive genetic change could occur at this rate (Fabry V.J. et al., 2008). In general, longer generation times of population afford decreased opportunities for evolutionary adaptation (Fabry V.J. et al., 2008; Byrne M., 2011). In addition, the potential for the development and adaptation may be irrelevant if the survival/abundance of the key associated (e.g. prey) species in their habitat would be compromised (Byrne M., 2011).

2. Change in distribution

   Ocean acidification and shoaling of aragonite saturation horizons will affect distribution of pteropods, among first the species living in the polar regions, restricted to aragonite-saturated waters (Orr C.J. et al., 2005; Seibel B.A. et al., 2007; Fabry V.J. et al., 2008; McNeil B.I. and Matear R.J., 2008). Their habitat will become increasingly vertically and geographically limited (Orr C.J. et al., 2005). Pteropods are expected to migrate to water depths or ocean regions less impacted by ocean acidification to escape the aragonite undersaturation conditions, which means their global and vertical distribution might drastically change in the future, such as shifting their distribution northwards in the Southern ocean (Hunt B.P.V. et al., 2008; McNeil B.I. and Matear R.J., 2008; Comeau S. et al., 2011; Bednaršek N. et al., 2012b). However, high-latitude pteropods migrating towards equator to warmer supersaturated regions will be

limited by their adaptations to low temperatures (Seibel B.A. et al., 2007; Fabry V.J. et al., 2008; Byrne M., 2011). Moreover, if pteropods will be forced to change their depth migration range due to shoaling aragonite horizons, thus unable to migrate into deep waters during the day to avoid predation, the survival rate of pteropods, particularly juveniles will drop (Comeau S. et al., 2011; Seibel B.A., 2011).

3. Disappearance

   If the shelled pteropods fail to adapt to the changed ocean chemistry conditions as well as show the inability to survive in warmer regions and remain a competitive group under the selective pressure, they will most likely begin to disappear first from the polar oceans and eventually from the larger ocean regions (Byrne M., 2011; Comeau S. et al., 2011; Bednaršek N. et al., 2012b).

5.1.3.2 Predictions for specific areas

The high latitude regions are expected to be most strongly and very early impacted by the ocean acidification and with continuous increase in CO_2 emissions (under IS92a/A2 SRES IPCC high emission scenarios) the entire water column in the Arctic and the Southern Ocean could become undersaturated already during this century (Orr C.J. et al., 2005; McNeil B.I. and Matear R.J., 2008; Steinacher M. et al., 2009). Since high latitude regions have naturally lower carbonate concentration, in the Arctic usually $2>\Omega_{ara}$ (Orr C.J. et al., 2005; Steinacher M. et al., 2009), the change needed to reach undersaturation is relatively small (Gruber N., 2011). In the high latitudes, in the Southern Ocean (south of the Polar Frontal Zone), pH and CO_3^{-2} saturation naturally decreases in wintertime because of cooling, which results in higher solubility of CO_2 and greater upwelling of deep water, high in dissolved organic carbon (Orr C.J. et al., 2005; McNeil B.I. and Matear R.J., 2008). The undersaturation in the high latitudes is thus predicted to be reached in the winter at the earliest (Orr C.J. et al., 2005); in the Southern Ocean, surface aragonite undersaturation is predicted to occur by the year 2030 (McNeil B.I. and Matear R.J., 2008), while in the Arctic localised undersaturation could commence as early as 2016 (Steinacher M. et al., 2009). However, a high regional variability in the amplitude and onset of the seasonal pH and CO_3^{-2} change was observed in the Southern Ocean (McNeil B.I. and Matear R.J., 2008), also indicating that in certain areas undersaturation could occur earlier than in other areas. This has been confirmed by Bednaršek N. et al. (2012b) study showing that surface aragonite undersaturation due to anthropogenic CO_2 is the case of presence in the first decade of the 21st century. Similarly, the rate of change in ocean chemistry is expected to differ between different areas in the Arctic Ocean due to different physical-chemical water properties, such as decreased alkalinity in the localised freshwater input as a result of sea ice melting, increased precipitation and river inflow (Steinacher M. et al., 2009; Yammamoto-Kawai M. et al., 2009; Comeau S. et al., 2011). Consequently, in certain parts of the Arctic and Southern Ocean, shelled pteropods (*Limacina helicina*) will become unable to precipitate $CaCO_3$ due to aragonite undersaturation throughout their whole vertical distribution range of upper 200 m already in the second half of this century (Comeau S. et al., 2011). However, acknowledging that in live animals dissolution starts at $\Omega \approx 1$ already (Bednaršek N. et al., 2012b), dissolution as a process might outcompete calcification from this decade onwards already.

On the contrary, in temperate, tropical and subtropical surface waters, larger absolute changes in surface aragonite saturation are projected for the 21st century, but due to

higher natural present-day carbonate ion concentrations (surface Ω_{ara} ~4), saturation horizons will remain deep, such as at 1500 m in the tropical Pacific, extending below the pteropod vertical migration zone (Orr C.J. et al., 2005; Steinacher M. et al., 2009; Comeau S. et al., 2011). In the North Pacific and North Atlantic (north of 50° N), models predict the aragonite saturation horizon will shoal profoundly (Orr C.J. et al., 2005) - in the North Atlantic from 3250 m to 1300 m (under A2 scenario) (Steinacher M. et al., 2009). However, as some subarctic regions in the North Pacific, where aragonite saturation horizons are already among the shallowest existing globally, might become undersaturated through the entire water column (under the IS29a scenario), the surface layers in the North Atlantic will remain saturated, due to the naturally deeper aragonite horizons (Feely et al. 2004, 2008; Orr C.J. et al., 2005; Steinacher M. et al., 2009). In the coastal North Pacific, periods of enhanced seasonal aragonite undersaturation associated with upwelling of undersaturated waters have already been documented (Feely R.A. et al., 2008). A decrease in aragonite saturation state was documented in Canada basin of the Arctic Ocean as a direct consequence of melting of sea ice and enhanced upwelling of aragonite undersaturated water (Yamamoto-Kawai M. et al., 2009).

5.1.3.3 Comparison of predicted trends and current observations

In high latitudes between 80-70° in the SH, particularly in the area south of the Antarctic Polar Front (APF) in the Southern Ocean and the Arctic Ocean, mean biomass concentrations of pteropods were high (27.2 mg C m^{-3}) in comparison with the majority of the other latitudinal belts (Bednaršek N. et al., 2012c). This is in accordance with previous observations showing high abundances of pteropods in the polar ecosystems, thus making them functionally important part of zooplankton community there (Boysen-Ennen E. et al., 1991; Cabal J.A. et al., 2002; Honjo S., 2004; Hunt B.P.V. et al., 2008). However, just 10° equatorward, mean calculated biomass concentration between 70-60° in both hemispheres was low (0.09 mg C m^{-3} in SH and 0.31 mg C m^{-3} in NH) (Bednaršek N. et al., 2012c). In the Southern Ocean, the reason for low concentrations might be naturally lower pH and CO_3^{-2} concentrations in the wintertime as well as in the summertime in this area (McNeil B.I. and Matear R.J. 2008). Furthermore, between 60-50° S, in the sub-Antarctic area of higher pH and CO_3^{-2} concentrations (north of the Antarctic Polar Front) (McNeil B.I. and Matear R.J., 2008), the results of this study demonstrated that biomass increases for the second time (13.93 mg C m^{-3}). Stark differences in biomass concentrations are likely to be a reflection of seasonally existing regional differences in aragonite (under)saturation state across latitudinal bands in the Southern Ocean. Following, pteropods are clearly less successful in the areas with seasonal low aragonite saturation or undersaturation, a near-future trend expected for the majority of the high-latitude ocean ecosystems (McNeil B.I. and Matear R.J., 2008; Comeau S. et al., 2011). In the high latitudes, the most common shelled pteropod is *Limacina helicina* that as a result of predominant juvenile population demographics overwinters in larvae or juvenile forms, with only 2% adults contributing to the populationin the Southern Ocean (Bednaršek N. et al., 2012a). Consequently, juveniles of *Limacina helicina* are exposed to lowest $CaCO_3$ concentration in their most vulnerable life stage - during important veliger larval development when their shells are thinner and consequently more fragile and prone to fragmentation (Bednaršek N., 2010; Comeau S. et al., 2010b; Lischka S. et al., 2011). Nevertheless, low aragonite saturation in high latitudes during the winter (McNeil B.I. and Matear R.J., 2008) affecting the survival of pteropod larvae might already be the cause of lower biomass concentrations recorded in between 70-60° S (Bednaršek N. et al., 2012c). As the entire water column south of APF (60° S) is expected to become

undersaturated with respect to aragonite by the end of 21st century (Orr C.J. et al., 2005; McNeil B.I. and Matear R.J., 2008), this might force adult pteropods to migrate northwards of the APF before spawning (Seibel B.A. et al., 2007; Fabry V.J. et al., 2008). The changes in the saturation north of APF are expected to be delayed due to the naturally higher pH and CO_3^{2-} levels and smaller fluctuation amplitudes during different seasons (Orr C.J. et al., 2005; McNeil B.I. and Matear R.J., 2008).

The connection between the vertical distribution of pteropods and aragonite saturation horizons is less clearly reflected in the results of this study. According to the recent *in situ* observation based models, current annual mean undersaturation horizon with respect to aragonite in the Arctic Ocean is located below 2000 m, with very low saturation in the near surface water layers, between 0-150 m (Steinacher M. et al., 2009). Moderately high biomass concentrations of pteropods were frequently recorded between 0-500 m and also below 500 m in the Arctic Ocean (Bednaršek N. et al., 2012c). Based on these results we can presume that pteropod vertical range and aragonite saturation horizons coincide. However, pteropods must be (locally, near the surface) already exposed to undersaturated conditions within their vertical migration range. Similarly, there are records of pteropods appearing (in smaller concentrations) between 25-200 m in the eastern North Pacific Ocean (Bednaršek N. et al., 2012c), were they might thus be also already experiencing undersaturated conditions as the undersaturation begins below 100-300 m and the undersaturated water seasonally even reaches the near surface (40-120 m) waters due to the upwelling (Feely R.A. et al., 2008). However, better distribution of depth aligned with carbonate chemistry is necessary to understand their vertical migration into undersaturated regions. Furthermore, there are no data records of pteropods in the Southern Ocean below 500 m (Bednaršek N. et al., 2012c), which could be an indication of their dwelling above the present aragonite saturation horizon occurring on average at 730 m (mostly below 1000 m) (Orr C.J. et al., 2005; Bednaršek N. et al., 2012b). However, Bednaršek N. et al., (2012b) observed local exposure to near saturation conditions in the upper 200 m *Limacina helicina antarctica* Scotia Sea (Southern Ocean) was already underway, resulting in dissolution of the shells of *Limacina helicina* specimen. Localised near saturation conditions above 400 m in the Southern Ocean occur due to seasonal upwelling of deep water, with low Ω_{ara} (McNeil B.I. and Matear R.J., 2008; Bednaršek N. et al., 2012b). The aragonite saturation horizons in the other ocean regions remain deep, and the correlation with pteropod vertical distribution is not evident from the obtained results. The regional shoaling of aragonite saturation horizons in ocean basins, such as Indian Ocean and mid- and low latitude regions in the Pacific and Atlantic Ocean (Feely R.A. et al., 2004), compared with pteropod distributions in that regions across time, might reveal some patterns. To sum up, due to the shoaling aragonite saturation horizons in all ocean basins, a change in migration range of pteropods is expected in the near future.

5.1.4 Interactions of environmental stressors

The interactive impact of multiple environmental stressors (warming, elevated pCO_2, hypoxia) on physiology and behaviour of marine organisms presents a major knowledge gap even though in reality these are the circumstances marine organisms will inevitably have to face in the future (Raven J. et al., 2005; Pörtner H.-O. 2008, 2010; Widdicombe S. and Spicer J.I., 2008; Hoffman G.E. and Todgham A.E., 2010; Byrne M., 2011; Kroeker K.J., 2011; Gruber N., 2011). Predicting the response of pteropods in multi-stressor environment is a complex task, since compensation to one

stressor can positively or negatively affect sensitivity or ability of animals to effectively response to another stressor (Pörtner H.-O. 2008, 2010; Hoffman G.E. and Todgham A.E., 2010).

Synergistic effects of environmental factors can dramatically alter the sensitivity and response of an individual physiology to hypercapnia (Widdicombe S. and Spicer J.I., 2008). There is some evidence that in some marine calcifying organisms, such as corals and echinoderms, low levels of warming can diminish negative impacts of acidification (Byrne M., 2011). In case of pteropods, acidification was shown to impact them directly via metabolic suppression due to elevated pCO_2 levels (Maas A.E. et al., 2012a; Seibel B.A. et al., 2012). However, at simultaneously elevated temperature and pCO_2 an increased metabolic rate was recorded (Comeau S. et al., 2010a). Based on the study performed on *Limacina helicina* juveniles, Lischka S. et al. (2011) suggested that perhaps at higher temperature due to related higher metabolic rate *Limacina helicina* might be able to counteract shell dissolution, by so-called ''repair'' calcification and avoid perforation of the shell at least for a certain amount of time. However, further studies need to address a pertinent topic on calcification vs. dissolution to examine to what extent can additional metabolic costs and trade-offs for maintaining the shell integrity under aragonite undersaturation be tolerated without seriously threatening the success of their development and reproduction and consequently the stability of pteropod population (Comeau S. et al., 2010a; Lischka S. et al., 2011).

As discussed before, pteropods will be forced to change their vertical distribution and migration patterns, because of the rising temperatures, shoaling of aragonite saturation horizons and spreading of the OMZs (Fabry V.J. et al., 2008; Seibel B.A. and Dierssen H.M., 2009; Comeau S. et al., 2011; Seibel B.A., 2011). Pteropods from high latitudes under aragonite undersaturated conditions might be limited in their equatorward migration due to their adaptation to cold temperatures and inability to tolerate warmer conditions at lower latitudes (Hoffman G.E. and Todgham A.E., 2010; Comeau S. et al., 2011; Rosenthal J.J.C. et al., 2012). On the other hand, pteropods from the temperate regions moving poleward due to the rising temperatures will be limited by the spreading aragonite undersaturation (Orr C.J. et al., 2005; Comeau S. et al., 2011). Furthermore, pteropods migrating to shallower, better oxygenated and aragonite saturated waters will be faced with warming environment closer to the surface (IPCC, 2007; Gruber N., 2011), which will be particularly stressful for temperature sensitive species, such as *Crescies virgula* (Maas et al., 2012b). The exposure of animals to their thermal extremes might enhance their sensitivity to elevated CO_2 levels and hypoxia (Pörtner H.-O. 2008, 2010). Therefore, as the threshold for stress at hypoxia in addition to O_2 concentration also depends on the level of CO_2 and temperature (Pörtner H.-O. and Farell A.P., 2008; Brewer P.G. and Peltzer E.T., 2009), the more temperature sensitive species, normally successfully surviving hypoxia at lower temperatures, may be less successful tolerating hypoxia at warmer temperatures due to higher energetic demands and thus life costs for organisms in warmer environment (Maas et al., 2012b). Additionally, elevated CO_2 levels and hypoxia might reduce thermal tolerance and enhance the sensitivity to the thermal extremes of marine organisms, due to a decreased functionality of tissues important for oxygen supply and body pH regulation capacity when affected by CO_2 or low oxygen concentration (Pörtner H.-O., 2008). This could additionally narrow geographical and vertical distribution range of pteropods by decreasing their ability to inhabit warmer surface waters or migrate into warmer latitudes.

The tolerance of different pteropod species through their life histories of longer-term exposure to different types of environmental stressors and the correlations/synergies

between the effects of the stressors remain to be studied in more detail, particularly for the very early life stages, as the impact of climate change on adult organisms is not accurate unless the bottlenecks of early in their life stage are considered (Byrne M., 2011).

5.2 Potential consequences of pteropod disappearance in the marine ecosystems

If the ecological and biogeochemical roles of pteropods in the marine ecosystems are taken into account, the changes in pteropod abundances, distribution or a disappearance of pteropods could have some consequences for marine ecosystem communities and biogeochemical cycles.

A decrease in the abundance of pteropods or in their calcification rates could mean a reduction in inorganic carbon flux to the deep ocean, shallower remineralisation of organic carbon and thus, consequently a reduction of the recycling time of CO_2 to the atmosphere as pteropods act as ballast material (Hunt B.P.V. et al., 2008; Manno C. et al., 2010; Pinsonneault A.J. et al., 2012). A decrease in pteropod contribution to total $CaCO_3$ flux might have a more pronounced impact in the environments where other $CaCO_3$ producers (coccolithophores and foraminifers) are less abundant, such as in Southern Ocean (Accornero A. et al., 2003; Gangstø R. et al., 2008; Bednaršek N. et al., 2012b). Gangstø R. et al. (2008) predicted a 65% decrease in aragonite production in polar and subpolar areas (>40°) by 2100, where aragonite dissolution is projected to increase for 72%. If biological carbon pump is affected as a result of pteropods loss, the strength of the ocean as a carbon sink might be affected (Feely R.A. et al., 2004; Manno C. et al., 2010; Pinsonneault A.J. et al., 2012). In addition, shallower remineralisation of organic matter could subsequently lead to oxygen depletion in the surface waters (Gruber N., 2011).

The loss of an important prey item for higher trophic levels may introduce changes within the trophodynamic system, with particularly negative consequences for monophagus gymnosomes (exclusively relying on thecosomatous pteropods as a food source) (Lalli C.M. and Gilmer R.W., 1989; Seibel B.A. et al., 2007; Hunt B.P.V. et al., 2008) and a new pressure for species that would become a substitute prey instead of pteropods (Fabry V.J. et al., 2008; Comeau S. et al., 2011). In case of the migrations to warmer tropical regions, gymnosomes would probably follow their prey, increasing the change in the food webs of marine ecosystems (Fabry V.J. et al., 2008). The loss of pteropod contribution as grazers of phytoplankton (blooms) might further affect marine ecosystem trophic dynamics (Fabry V.J. et al., 2008), as pteropods can represent an important part of top-down control of phytoplankton blooms (Elliot D.T. et al., 2009; Pakhomov E.A. and Froneman P.W., 2004; Bernard K.S., 2006).

It is difficult to predict and quantify the exact consequences of the loss of one group of organisms such as pteropods from the ecosystem and we can only vaguely phantom what impact it will have on the ecosystem community structure or to what extent it will affect the services of the ecosystems, such as the biological carbon pump (Raven J. et al., 2005; Hunt B.P.V. et al., 2008). There is a general lack of knowledge how climate change driven synergistic environmental stressors can affect marine biota, which we are only beginning to understand (e.g. Raven J. et al., 2005; Hoffman G.E. and Todgham A.E., 2010; Pörtner H.-O., 2010; Byrne M., 2011; Gruber N., 2011; Kroeker K.J., 2011; Seibel B.A. et al., 2012). However, what remains certain is that interactive

effects of multiple stressors and the complex biological and ecological responses could result in significant loss of marine biodiversity and introduce substantial changes in the ecosystem regimes (Orr C.J. et al., 2005; Fabry V.J. et al., 2008; Byrne M., 2011; Kroeker K.J., 2011). Using modelling approach for the simulation of ocean ecosystem dynamics by incorporating PTFs, including pteropods, can advance the understanding of pteropod absence in the ecosystems and the impact of climate change driven environmental stressors on the marine ecosystems in general (Le Quéré C. 2005, 2009). Moreover, other environmental stressors accelerated by human activities like nutrient enrichment, overfishing, invasive species and pollution should also be taken into account to gain more comprehensive insight in changes in marine ecosystems (Fabry V.J. et al., 2008; Byrne M., 2011; Gruber N., 2011; Maas A.E. et al., 2011).

5.3 A glimpse into the future

Currently available data and knowledge about pteropods provided a valuable insight into pteropod presence and role in the marine ecosystems, confirming the importance of these marine animals as a studying case in the light of the future global ocean changes. More so, because pteropods present an important plankton functional type in the marine ecosystems (Hood R.R. et al., 2006) predicted to be very early impacted by the climate change driven environmental stressors (e.g. Orr C.J. et al., 2005; Fabry V.J. et al., 2008).

Besides laboratory mesocosm experiments, behaviour and responses of marine organisms to specific conditions and broader responses to environmental stressors on a community/ecosystem level can be predicted through extensive *in situ* monitoring that could and should become a primary tool in demonstrating the early onset of ocean changes, such as acidification (Fabry V.J. et al., 2008; Gruber N., 2011, Bednaršek N. et al., 2012b). There are certain ocean regions where aragonite saturation horizons have already notably shoaled, especially in parts of the Southern Ocean, the equatorial Atlantic and in the North Pacific (Feely R.A. et al. 2004, 2008; Orr C.J. et al., 2005; Steinacher M. et al., 2009). These are valuable *in situ* testing areas for observational research of marine ecosystems and organisms in question, responding to shoaling of aragonite horizons. An exemplary case of *in-situ* observational research was conducted by Bednaršek N. et al. (2012b) on live *Limacina helicina* showing signs of shell dissolution in its natural environment in the Southern Ocean. This study revealed the impact of aragonite undersaturation long before the projected dates (Bednaršek N. et al., 2012b), indicating how limited is our understanding of the complexity and unpredictability of the global changes in the natural environment (Gruber N., 2011). Similarly, naturally occurring stressful environments, such as OMZs can also serve as study sites for *in-situ* observation of physiological and behavioural responses (Fabry V.J. et al., 2008; Maas A.E. et al. 2012a, 2012b).

Furthermore, in the natural environment, the intensity and scale of changes caused by environmental stressors is expected to affect pteropods differently during specific seasons (McNeil B.I. and Matear R.J., 2008; Orr C.J. et al., 2005; Seibel B.A. et al., 2012). It is thus important to observe pteropod population fluctuations through all the seasons with an aim to recognize the changes in biological responses or timing of certain events throughout their life histories (e.g. Seibel B.A. et al., 2012). Furthermore, latent effects of exposure to environmental stressors are possible, i.e. the history of exposure to environmental stressors such as acidification/hypercapnia can compromise thermal tolerance or sensitivity of animals to hypoxia (Byrne M., 2011).

From all stated, it is uttermost important for data to be systematically collected during all the seasons, across longer time periods and various regions, especially due to high spatial variability of natural environmental conditions which can accelerate or delay deleterious effects caused by environmental stressors (McNeil B.I. and Matear R.J., 2008; Seibel B.A. et al., 2012).

Moreover, the understanding of the interactive impact of acidification, deoxigenation and ocean warming on biogeochemistry and ecosystems is limited and future research requires coordinated multidisciplinary approach of detailed laboratory studies, *in situ* experiments and observations, large-scale/long-term monitoring, all combined with the modelling attempts (Le Quéré C. et al. 2005, 2009; Fabry V.J. et al., 2008; Widdicombe S. and Spicer J.I., 2008; Gruber N., 2011; Seibel B.A., 2012).

Research being done on pteropods is a small part in the multidisciplinary research done on the topic of ocean ecosystem functioning, ocean biochemistry and climate change driven alterations in the oceans, such as acidification. It is also essential that all research done has the highest level of quality and comparability. European Project on Ocean Acidification (EPOCA) developed a Guide for Best Practices in Ocean Acidification Research and Data Reporting, standardized protocols for observations and experimental research, measurements and data reporting (Riebesell U. et al., 2010). It is accessible to wider community with the plan for regular update with the purpose to ensure comparability and quality of the vast amount of data being generated by the expanding research in this marine science field (Riebesell U. et al., 2010). The ongoing research on pteropods will consistently follow this or similar kind of directives.

Finally, the created MAREDAT pteropod biomass database is the first attempt to combine all available abundance/biomass data of pteropods currently available and enables estimates about global distribution of pteropods and their contribution to the carbonate cycle to be assessed. The database should be continually updated to provide a better tool for modellers of ecosystem processes, global biogeochemical cycles and the effects of ocean acidification and other stressors on pteropods and other calcifying species in the future.

6 CONCLUSION

Pteropods, as it was shown throughout the literature review in this study, play an important ecological role in marine ecosystems and can substantially contribute to biogenic inorganic and organic fluxes, which is why they should be incorporated into biogeochemical models – DGOMs (Hood R.R. et al., 2006; Le Quere C. et al., 2009). However, adding complexity and PFTs to biogeochemical or ecosystem models and increasing the number of parameters that cannot be constrained with the available data can lead to a decrease in predictive ability of the models (Hood R.R. et al., 2006). Therefore, in order to include pteropods in the model schemes and for model validation, an adequate amount of data on pteropod carbon biomass, abundance and their physiological parameters was required. Within this diploma thesis, the available information on pteropods was gathered and a first global pteropod carbon biomass database was created, additionally complemented with the existing physiological data. While data on abundance and biomass was used in this study, the physiological data remains to be included into models as this fell outside of this diploma thesis scope. It represents a valuable pre-basis for the modelling work, which is to be carried out in cooperation with modelling experts in this field, Dr. Eric Buitenhuis and Prof. Corrine Le Quéré of the University of East Anglia.

In addition, this study showed and confirmed that pteropods are functionally important group of plankton (PFTs), due to their contribution to the global carbon biomass production and global carbonate budget. In comparison with previously done assessments, the results of this study indicate the contribution of pteropods to global carbon/carbonate budget was possibly underestimated. Therefore, a reassessment of global carbon/carbonate production may be required in order to assign pteropods a new position among the main contributors.

Furthermore, the impacts of ocean acidification, ocean deoxygenation and ocean warming on pteropods were assessed. Through the results of the abundance and biomass data analysis, the dynamics in the distribution and seasonal fluctuations in biomass concentrations of pteropod populations in correlation with physical and biological environmental factors (e.g. temperature, oxygen abundance, aragonite saturation, food abundance) were established. The long-term changes in populations that might be correlated to changing environment (warming, deoxygenation, shoaling of aragonite horizons) over the time range (1950-2000) covered by the data collected in this study, were not discussed, as this was outside the scope of this study. However, based on the assessed data, I conclude pteropods are susceptible to the effects of all three environmental stressors driven by the global climate change and their inevitable synergetic pressure, which will result in changes in the geographical and vertical distribution as well as the abundances of pteropods. It seems it will possibly relatively soon lead to disappearance of pteropods from certain ocean regions, which could have significant ecological consequences for marine trophic systems as well as biochemical cycles, such as the ocean carbon pump, with implications for the strength of the oceans as the CO_2 sink.

7 REFERENCES

Abercrombie M., Hickman M., Johnson M.L., Thain M. 1992. The Penguin Dictionary of Biology. 8th edition, The Penguin Reference Books, Penguin Group, Penguin Books Ltd, London, England: pp. 43, 357, 492

Accornero A., Manno C., Esposito F., Gambi, M. C. 2003. The vertical flux of particulate matter in the polyna of Terra Nova Bay. Part II. Biological components. *Antarctic Science*, 15, 175-188

Almogi-Labin A., Hemleben C., Deuser W.G. 1988. Seasonal variation in the flux of euthecosomatous pteropods collected in a deep sediment trap in Sargasso Sea. *Deep-Sea Research*, 35, 3: 441-464

Andersen V., Sardou J., Gasser B. 1997. Macroplankton and mikronekton in the northeast tropical Atlantic: abundance, community composition and vertical distribution in relation to different trophic environments. Deep-Sea Research I, 44, 2: 193-222

Anderson T.R. 2005. Plankton functional type modelling: running before we can walk?. *Journal of Plankton Research*, 27, 11: 1073-1081

Armstrong R.A., Lee C., Hedges J.I., Honjo S., Stuart G.W. 2002. A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals. *Deep-Sea Research II*, 49, 219–236

Armstrong J. L., Boldt J. L., Cross A. D., Moss J. H., Davis N. D., Myers K. W., Walker R. V. et al. 2005. Distribution, size, and interannual, seasonal and diel food habits of northern Gulf of Alaska juvenile pink salmon, Oncorhynchus gorbuscha. *Deep Sea Research II*, 52, 247–265

Ashjian C.J., Cabell S.D., Gallager S.M., Alatalo P. Distribution of plankton, particles, and hydrographic features across Georges Bank described using the Video Plankton Recorder. *Dee-Sea research Part II*, 48, 245-282

Balch W.M., Kilpatrick K.A. 1996. Calcification rates in the equatorial Pacific along 140 °W: *Deep Sea Research Part II*, 43, 971-993

Balch W.M., Drapeau D.T., Bowler B.C., Booth E. 2007. Prediction of pelagic calcification rates using satellite measurements. *Deep-Sea Research II*, 54, 478-495

Bandel K., Hemleben C. 1995. Observations on the ontogeny of thecosomatous pteropods (holoplanktic Gastropoda) in the southern Red Sea and from Bermuda. *Marine Biology*, 124, 225-243

Barnett T.P, Pierce D.W., AchutaRao K.M., Glecker P.J., Santer B.D., Gregory J.M., Washington W.M. 2005. Penetration of Human-Induced Warming into World's Oceans. *Science,* 309, 284-287

Bathmann U.V., Noji T.T., von Bodungen B. 1991. Sedimentation of pteropods in the Norwegian Sea in autumn. *Deep-Sea Research*, 38, 10: 1341-1360

Balarin M.G., 1999. Size fractionated phytoplankton biomass and primary production in the Southern Ocean. M.Sc. Thesis, Rhodes University, Grahamstown

Bednaršek, N. 2010. Vulnerability of Southern Ocean pteropods to anthropogenic ocean acidification. PhD. University of East Anglia. School of Environmental Sciences

Bednaršek N., Tarling G.A., Bakker D.C.E. 2012a. Population dynamics and biogeochemical significance of *Limacina helicina antarctica* in the Scotia Sea (Southern Ocean). *Deep-Sea Research II: Topical Studies in Oceanography*, 59-60, 105-116

Bednaršek N., Tarling G.A., Bakker D.C.E., Fielding S., Jones E.M., Venables H.J., Ward P., Kuzirian A., Lézé B., Feely R.A., Murphy E.J. 2012b. Extensive dissolution of live pteropods in the Southern Ocean. *Nature Geoscience*, 5, 881-885, doi: 10.1038/ngeo1635

Bednaršek N., Možina J., Vogt M., O'Brien C., Tarling G.A. 2012c. The global distribution of pteropods and their contribution to carbonate and carbon biomass in the modern ocean. *Earth System Science Data,* 4, 167-186

Behrenfeld M.J., O'Malley R.T., Siegel D.A., McClain C.R., Sarmiento J.L., Feldman G.C., Milligan A.J., Falkowski P.G., Letelier R.M., Boss E.S. 2006. Climate-driven trens in contemporary ocean productivity. *Nature, Letters*, 444, doi: 10.1038/nature05317

Benfield M.C., Davis C.S., Wiebe P.H., Gallager S.M., Lough R.G., Copley N.J. 1996. Video Plankton Recorded estimates of copepod, pteropod and larvacean distributions from a stratified region of Georges Bank with comparative measurements from a MOCNESS sampler. *Deep-Sea Research II*, 43, 7-8: 1925-1945

Berelson W.M., Balch W.M., Feely R.A., Sabine C., Lee K. 2007. Relating estimates of $CaCO_3$ production, export and dissolution in the water column to measurements of $CaCO_3$ rain into sediment traps and dissolution on the sea floor: a revised global carbonate budget. *Global Biogeochemical Cycles*, 21, GB1024

Berner R.A., Honjo S. 1981. Pelagic sedimentation of aragonite: its geochemical significance. *Science*, 3, 940–942

Bernard K.S., Froneman P.W. 2005. Trophodynamics of selected mesozooplankton in the west-Indian sector of the Polar Frontal Zone, Southern Ocean. *Polar Biology,* 28, 594-606, doi: 10.1007/s00300-005-0728-3

Bernard K. S. 2006. The role of the euthecosome pteropod *Limacina retroversa*, in the Polar Frontal Zone, Southern Ocean. PhD. Rhodes University.

Bernard K.S., Froneman P.W. 2009. The sub-Antarctic euthecosome pteropod, *Limacina retroversa*: Distribution patterns and trophic role. *Deep-Sea Research I*, 56, 582-598

Biggs D.C. 1977. Respiration and ammonium excretion by open ocean gelatinous zooplankton. *Limnology and Oceanography*, 22, 1

Blachowiak-Samolyk K., Søreide J.E., Kwasniewski S., Sundfjord A., Hop H., Falk-Petersen S., Hegseth E.N. 2008. Hydrodynamic control of mesozooplankton

abundance and biomass in northern Svalbard waters (79-81 °N). *Deep-Sea Research II*, 55, 2210-2224

Bollens S.M, Frost B.W., Thoreson D.S., Watts S.J. 1992. Diel vertical migration in zooplankton: field evidence in support of the predator avoidance hypothesis. *Hydrobiologia*, 234, 1: 33-39

Boltovsky D. (Ed). 1999. South Atlantic Zooplankton; Volumes 1&2; Backhuys Publishers, Leiden, Netherlands

Boyce D.G., Lewis M.R., 2010. Worm B., Global phytoplankton decline over the past century. *Nature, Articles*, 499, 591-596, doi: 10.1038/nature09268

Boysen-Ennen E., Hagen W., Hubold G., Piatkowski U. 1991. Zooplankton biomass in the ice-covered Weddell Sea, Antarctica. *Marine Biology*, 111, 227-235

Brewer P.G., Peltzer E.T. 2009. Limits to marine life. *Science,* 324, 347–48

Brierley A.S., Thomas D.N. 2002. Ecology of southern ocean pack ice. *Advances in Marine Biology*, 43, 171-277

Broughton E.A., Lough R.G. 2006. A direct comparison of MOCNESS and Video Plankton Recorder zooplankton abundance estimates: Possible application for augmenting net sampling with video systems. *Deep-Sea Research II,* 53, 2789-2807, doi: 10.1016/j.dsr2.2006.08.013

Bruland K.W., Silver M.W. 1981. Sinking Rates of Faecal Pellets from Gelatinous Zooplankton (Salps, Pteropod, Doliolids). *Marine Biology*, 63, 295-300

Bryan P.J., Yoshida W.Y., McClintock J.B., Baker B.J. 1995. Ecological role for pteroenone, a novel antifeedant from the conspicuous antarctic pteropod *Clione antarctica* (Gymnosomata: Gastropoda). *Marine Biology*, 122, 2: 271-277

Böer M., Gannefors C., Kattner G., Graeve M., Hop H., Falk-Petersen S. 2005. The Arctic pteropod *Clione limacina*: seasonal lipid dynamics and life-strategy. *Marine Biology*, 147:707-717

Böer M., Kattner G., Graeve M. 2006. Impact of feeding and starvation on the lipid metabolism of the Arctic pteropod *Clione limacina. Journal of Experimental Marine Biology and Ecology*, 328, 98-112

Böer M., Graeve M., Kattner G. 2007. Exceptional long-term starvation ability and sites of lipid storage of the Arctic pteropod *Clione limacina*. *Polar Biology*, 30, 571-580

Buitenhuis E. T., Vogt, M., Bednaršek N., Doney S.C., Leblanc C., Quéré C.L., Luo Y.-W. , Moriarty M., O'Brien C., O'Brien T., Peloquin J., Schiebel R. 2012a (under review): MAREDAT : Towards a World Ocean Atlas of MARine Ecosystem DATa. *Earth Systems Science Data (Open Access Discussions)*, 5, 1077-1106, doi:10.5194/essdd-5-1077-2012

Buitenhuis E.T., Li W.K.W., Vaulot D., Lomas M.W., Landry M., Partensky F. Karl D.M. et al. 2012b. Picophytoplankton biomass distribution in the global ocean. *Earth Systems Science Data (Open Access Discussions), 5, 221-242*

Buitenhuis E.T., Li W.K.W., Lomas M.W., Karl D.M., Landry M.R., Jacquet S. 2012c. Bacterial biomass distribution in the global ocean. *Earth Systems Science Data,* 4, 101-106, doi:10.5194/essd-4-101-2012

Byrne R.H., Acker J.G., Betzer P.R., Feely R.A., Cates M.H. 1984. Water column dissolution of aragonite in the Pacific Ocean. *Nature*, 312, 321-326

Byrne M. 2011. Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. *Oceanography and Marine Biology: An annual review*, 49, 1-42

Cabal J.A., Alvarez-Marqués Fl., Acuña J.L., Quevedo M., Gonzalez-Quirós, Huskin I., Fernández D., del Valle C.A., Anadón R. 2002. Mesozooplankton distribution and grazing during the productive season in the Northwest Antarctic Peninsula (FRUELA cruises). *Deep-Sea Research II,* 49, 869-882

Caldeira K., Wickett M. E. 2003. Anthropogenic carbon and ocean pH. *Nature,* 425, 365, doi:10.1038/425365a

Chauvaud L., Thompson J.K., Cloern J.E., Thouzeau G. 2003. Clams as CO_2 generators: the *Potamocorbula amurensis* example in San Francisco Bay. *Limnology and Oceanography*, 48, 2086-2092

Chen C., Bé A.W.H. 1964. Seasonal distributions of euthecosomatous pteropods in the surface waters of five stations in the western North Atlantic. *Bulletin of Marine Science Gulf and Caribbean*, 14, 185–220

Chen B., Landry M.R., Huang B., Liou H. 2012. Does warming enhance the effect og microzooplankton grazing on marine phytoplankton in the ocean?. *Limnology and Oceanography*. 57, 2: 519-526, doi: 10.4319/lo.2012.57.2.0519

Christou E.D., Moraitou-Apostolopoulou M. 1995. Metabolism and feeding of mesozooplankton in the eastern Mediterranean (Hellenic coastal waters). *Marine Ecology Progress Series*, 126, 39-48

Clarke C., Roff J.C. 1990. Abundance and Biomass of Herbivorous Zooplankton off Kingston, Jamaica, with Estimates of their Annual Production. *Estuarine, Coastal and Shelf Science,* 31, 423-437

Collier R., Dymond J., Honjo S., Manganini S., Francois R. 2000. The vertical flux of biogenic and lithogenic material in the Ross Sea: moored sediment trap observations 1996–1998. *Deep-Sea Research Part II,* 47, 3491–3520

Comeau S., Gorsky G., Jeffree R., Teyssié J.-L., Gattuso J.-P. 2009. Impact of ocean acidification on a key Arctic pelagic mollusc (*Limacina helicina*). *Biogeosciences*, 6, 1877–1882

Comeau S., Jefferee R., Teyssie J.-L., Gattuso J.-P. 2010a. Response of the Arctic Pteropod *Limacina helicina* to Projected Future Environmental Conditions. *PLoS ONE*, 5 (6)

Comeau S., Gorsky G., Alliouane S., Gattuso J. P. 2010b. Larvae of the pteropod *Cavolinia inflexa* exposed to aragonite undersaturation are viable but shell-less. *Marine Biology*, 157, 2341–2345

Comeau S., Gattuso J.-P., Nisumaa A.-M., Orr J. 2011. Impact of aragonite saturation state changes on migratory pteropods. *Proceedings of The Royal Scociety of London, Series B.: Biological Sciences,* 279, 732-738, doi: 10.1098/rspb.2011.0910

Connover R.J., Lalli C.M. 1972. Feeding and growth in *Clione limacina* (Phipps), a pteropod mollusk. *Journal of Exploration in Marine Biololgy and Ecology*, 9, 279–302

Cottier F.R., Tarling G.A., Wold A., Falk-Petersen S. 2006. Unsynchronised and synchronised vertical migration of zooplankton in a high Arctic fjord. *Limnology and Oceanography*, 51, 6: 2586-2599

Daase M., Eiane K. 2007. Mesozooplankton distribution in northern Svalbard waters in relation to hydrography. *Polar Biology,* 30, 969-981, doi: 10.1007/s00300-007-0255-5

Dadon J.R., de Cidre L.L. 1992. The reproductive cycle of the Thecosomatous pteropod *Limacina retroversa* in the western South Atlantic. *Marine Biology*, 114, 439-422

Daufresen M., Lengfellner K., Sommer U. 2009. Global warming benefits the small in aquatic ecosystems. *PNAS,* 106, 31, 12788-12793

Davis C.S., Wiebe P.H. 1985. Macrozooplankton Biomass in a Warm-Core Gulf Stream Ring: Time Series Changes in Size Structure, Taxonomic Composition, and Vertical Distribution. *Journal of Geophysical Research*, 90, C5: 8871-8884

Dierssen H.M. 2010. Perspectives on empirical approaches for ocean color remote sensing of chlorophyll in a changing climate. *Proceedings of National Academy of Sciences of USA,* 107, 40, 17073–17078

Dominigues C.M., Church J.A., White N.J., Glecker P.J., Wijffels S.E., Barker P.M., Dunn J.R. 2008. Improved estimates of upper-ocean warming and multi-decadal sea-level rise. *Nature, Letters*, 453, doi: 10.1038/nature07080

Doney S.C., Fabry V.J., Feely R.A., Kleypas J.A. 2009. Ocean acidification: the other CO_2 problem. *Annual Review of Marine Science*, 1, 169-192

Dvoretsky V.G., Dvoretsky A.G. 2009. Summer mesozooplankton distribution near Novaya Zemlya (eastern Barents Sea). *Polar Biology*, 32, 719-731, doi: 10.1007/s00300-008-0576-z

Elliot D.T., Tang K.W., Shields A.R. 2008. Mesozooplankton beneath the summer sea ice in McMurdo SOund, Antarctica: abundance, species composition, and DMSP content. *Polar Biology,* 32, 113-122

Fabry, V. J. 1989. Aragonite production by pteropod molluscs in the subarctic Pacific, Deep Sea Research Part A. *Oceanographic Research Papers*, 36, 11: 1735-1751

Fabry V.J. 1990. Shell growth rates of pteropod and heteropod molluscs and aragonite production in the open ocean: Implications for the marine carbonate system. *Journal of Marine Research*, 48, 209-222

Fabry V.J., Seibel B.A., Feely R.A., Orr C.J. 2008. Impacts of ocean acidification on marine fauna and ecosystem process. *ICES Journal of Marine Science*, 65, 414-432

Falk-Petersen S., Leu E., Berge J., Kwasniewski S., Nygård H., Røstad A., Keskinen E., Thormar J., von Quillfeldt C., Wold A., Gulliksen B. 2008. Vertical migration in high Arctic waters during autumn 2004. *Deep-Sea Research II*, 55, 2275-2284

Feely R. A., Byrne R.H., Acker J.G., Betzer P.R., Chen C.-T., Gendron J.F., Marilyn F.L. 1988. Winter-summer variations of calcite and aragonite saturation the northeast Pacific. *Marine Chemistry*, 25, 227-241

Feely R. A., Sabine C. L., Kitack L., Berelson W., Kleypas J., Fabry V. J., Millero F. J. 2004. Impact of Anthropogenic CO_2 on the $CaCO_3$ System in the Oceans. *Science*, 305, 5682: 362–366, doi: 10.1126/science.1097329

Feely R. A., Sabine C. L., Hernandez-Ayon J. M., Ianson D., Hales, B. 2008. Evidence for Upwelling of Corrosive ”Acidified” Water onto the Continental Shelf. *Science*, 320, 1490–1492, doi:10.1126/science.1155676, 2008

Fernandez de Puelles M.L., Alemany F., Jansa´ J. 2007. Zooplankton time-series in the Balearic Sea (Western Mediterranean): Variability during the decade 1994-2003. *Progress In Oceanography,* 74, 329-354, doi:10.1016/j.pocean.2007.04.009

Flores H., van Franeker J.-A., Cisewski B., Leach H., Van de Putte A.P., Meesters E. (H.W.G.), Bathmann U., Wolff W.J. 2011. Macrofauna under sea ice and in the open surface layer of the Lazarev Sea, Southern Ocean. *Deep-Sea Research II*, 58, 1948-1961

Fortier M., Fortier L., Hattori H., Saito H., Legendre L. 2001. Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. *Journal of Plankton Research*, 23, 11: 1263-1278

Forward R.B. 1988. Diel vertical migration: zooplankton photobiology and behaviour. *Oceanographical Biology Annual Review*, 26, 361-393

Foster, B.A. 1987. Composition and Abundance of Zooplankton Under the Spring Sea Ice of McMurdo Sound, Antarctica. *Polar Biology*, 8, 41-48

Francois R., Honjo S., Krishfield R., Manganini S. 2002. Factors controlling the flux of organic carbon to the bathypelagic zone of the ocean. *Global Biogeochemical Cycles,* 16, 4: 1087

Froneman P.W., Pakhomov E.A. 1998. Trophic importance of the chaetognaths *Eukrohnia hamata* and *Sagitta gazellae* in the pelagic system of the Prince Edward Islands (Southern Ocean). *Polar Biology,* 19, 242-249

Froneman P.W., Pakhomov E.A., Treasure A. 2000. Trophic importance of the hyperiid amphipod, *Themisto gaudichaudi*, in the Prince Edward Archipelago (Southern Ocean); *Polar Biology,* 23, 429-436

Froneman P.W., Laubischer R.K., Mcquaid C.D. 2001. Size-fractionated Primary Production in the South Atlantic and Atlantic Sectors of the Southern Ocean. *Journal of Plankton Research,* 23, 6: 611-622

Frölicher T.L., Joos F., Plattner G.K., Steinacher M., Doney S.C. 2009. Natural variability and anthropogenic trends in oceanic oxygen in a coupled carbon cycle-climate model ensemble. *Global biogeochemical Cycles,* 23, GB1003: 15, doi:10.1029/2008GB003316

Gangstø R., Gehlen M., Schneider B., Bopp L., Aumont O., Joos F. Modeling the marine aragonite cycle: changes under rising carbon dioxide and its role in shallow water CaCO3 dissolution. *Biogeosciences*, 5, 1057-1072

Gannefors C., Böer M., Kattner G., Graeve M., Eiane K., Gulliksen B., Hop H., Falk-Petersen S. 2005. The Arctic sea butterfly *Limacina helicina*: lipids and life strategy. *Marine Biology*, 147, 169-177

Gilmer R.W. 1972. Free-floating mucus webs: a novel feeding adaptation for the open ocean. *Science*, 176, 1239-1240

Gilmer, R.W. 1990. In situ observations of feeding in thecosomatous pteropod molluscs, *American Malacological Bulletin*, 8, 1: 53-59

Gilmer R.W., Harbison G.R. 1986. Morphology and field behaviour of pteropod molluscs: feeding methods in the families Cavoliniidae, Limacinidae and Peraclididae (Gastropoda: Thecosomata), *Marine Biology*, 91, 47-57

Gilmer R.W., Harbison G.R. 1991. Diet of *Limacina helicina* (Gastropoda: Thecosomata) in Arctic waters in midsummer, *Marine Ecology Progress Series*, 77, 125-134

Gilmer R., Lalli C. 1990. Bipolar variation in *Clione*, a gymnosomatous pteropod. *American Malacological Bulletin*, 8, 67-75

Gliwicz M.Z. 1986. Predation and the evolution of zooplankton population. *Limnology and Oceanography*, 24, 226-242

Glover, D. M., Jenkins, W.J. and Doney, S.C. 2011. Modeling Methods for Marine Science, Cambridge University Press, Cambridge, UK

Gruber N. 2011. Warming up, turning sour, losing breath: ocean biogeochemistry under global change. *Philosophical Transactions of the Royal Society A, Mathematical, physical & Engeneering Sciences*, 369, 1980-1996

Guppy M., Withers P. 1999. Metabolic depression in animals: physiological perspectives and biochemical generalizations. *Biological Reviews of Cambridge Philosophical Society*, 74, 1: 1-40

Harbison G.R., Gilmer R.W. 1992. Swimming, buoyancy and feeding in shelled pteropods – a comparison field and laboratory observations. *Journal of Molluscan Studies,* 58, 3: 337-339, doi: 10.1093/mollus/58.3.337

Harris R.P., Wiebe P.H., Lenz J., Skjoldal H.R., Huntley M. 2000. Zooplankton Methodology Manual. *Elsevier Academic Press*, London, UK: pp. 684

Harrison D.E., Carson M. 2006. Is the World Ocean Warming? Upper-Ocean Temperature Trends: 1950-2000. *Journal of Physical Oceanography*, 37, 174-187

Hofmann M., Schellnhuber H.-J. 2009. Oceanic Acidification affects marine carbon pump and triggers extended marine oxygen holes. *PNAS,* 106, 9: 3017-3022

Hofmann G.E., Todgham A.E. 2010. Living in the Now: Physiological Mechanisms to Tolerate a Rapidly Changing Environment. *Annual Review of Physiology*, 72, 127-45, doi: 10.1146/annurev-physiol-021909-135900

Holligan P.M., Charalampopoulou A., Hutson R. 2010. Seasonal distributions of the coccolithophore, *Emiliania huxleyi*, and of particulate inorganic carbon in surface waters ofthe Scotia Sea. *Journal of Marine Systems*, 82,195–205

Honjo S., Francois R., Manganini S., Dymond J., Collier R. 2000. Particle fluxes to the interior of the Southern Ocean in the Western Pacific sector along 170° W. *Deep Sea Research Part II,* 47, 3521–3548

Honjo S. 2004. Particle export and the biological pump in the Southern Ocean. *Antarctic Science*, 16, 501–516.

Honjo S., Manganini, S.J., Krishfield, R.A., Francois, R. 2008. Particulate organic carbon fluxes to the ocean iterior and factors controling the biological pump: a synthesis of global sediment trap programs since 1983. *Progress in Oceanography*, 76, 217-285

Hood R.R., Laws E.A., Armstrong R.A., Bates N.R., Brown C.W., Carlson C.A., Chai F., Doney S.C., Falkowski P.G., Feely R.A., Friedrichs M.A.M., Landry M.R., Moore J.K., Nelson D.M., Richarson T.L., Saluhoglu B., Schartau M., Toole D.A., Wiggert J.D. 2006. Pelagic functional group modelling: Progress, Challenges and prospects. *Deep-Sea Research II*, 53, 459-512

Hopkins T.L. 1987. Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Marine Biology*, 96, 93-106

Hunt, B.P.V., Hosie G.H. 2006. The seasonal succession of zooplankton in the Southern Ocean south of Australia, part I: The seasonal ice zone. *Deep-Sea Research I*, 53, 1182-1202, doi:10.1016/j.dsr.2006.05.001

Hunt B.P.V., Pakhomov E.A., Hosie G.W., Siegel V., Ward P., Bernard K. 2008. Pteropods in Southern Ocean ecosystems, *Progress in Oceanography.* 78, 3: 193-221

Hunt B., Strugnell J., Bednaršek N., Linse K., Nelson R.J., Pakhomov E., Seibel B., Steinke D., Wüzberg L. 2010. Poles Apart: The ‘’Bipolar’’ Pteropod Species *Limacina helicina helicina* Is Genetically Distinct Between the Arctic and Antarctic Oceans*. PLoS ONE*, 5, 3: e9835

Hays G.C., Kennedy H., Frost B.W. 2001. Individual variability in diel vertical migration of a marine copepod: why some individuals remain at depth when other migrate. *Limnology and Oceanography*, 46, 250-254

Iglesias-Rodriguez M.D., Armstrong R., Feely R.A., Hood J., Kleypas J.D., Milliman J.D., Sabine C., Sarmiento J. 2002. Progress made in the study of ocean's calcium carbonate budget. *EOS Transactions*, American Geophysical Union, 83, 374-375

Ikeda T. 1989. Are Antarctic zooplankton metabolically more cold-adapted than arctic zooplankton? An intra-genetic comparison of oxygen consumption rates. *Journal of Plankton research*, 11, 3: 619-624

IPCC - Climate change 2007: Working Group I: The physical science basis. IPCC Fourth Assessment Report: Climate Change 2007of the Intergovernmental Panel on Climate Change (Eds. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor & H. Miller). Cambridge, UK: Cambridge University Press

Jennings R.M., Bucklin A., Ossenbrügger H., Hopcroft R.R. 2010. Species diversity of planktonic gastropods (Pteropoda and Heteropoda) from six ocean regions based on DNA barcode analysis. *Deep-Sea Research II*, 57, 2199-2210

Juranek L.W., Russel A.D., Spero H.J. 2003. Seasonal oxygen and carbon isotope variability in euthecosomatous pteropods from the Sargasso Sea. *Deep-Sea Research I*, 50, 231-245

Karstensen J., Stramma L., Visbeck M. 2008. Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. *Progress in Oceanography,* 77, 331-350

Kattner G., Hagen W., Graeve M., Albers C. 1998. Exceptional lipids and fatty acids in the pteropod *Clione limacina* (Gastropoda) from both polar oceans. *Marine Chemistry*, 61, 219-228

Keeling R. F., Körtzinger A., Gruber N., 2010. Ocean deoxygenation in a warming world. *Annual Review of Marine Science*, 2, 199-229

Khatiwala S., Primeau F., Hall T. 2009. Reconstruction of the history of anhtopogenic CO_2 concentrations in the ocean. *Nature, Letters,* 462, doi: 10.1038/nature08526

Kirkup L. 2002. Data Analysis with Excel®: An Introduction for Physical Scientists. Cambridge University Press, 1st edition (March 18, 2002): pp. 184-186

Kobayashi, H.A. 1974. Growth cycle and related vertical distribution of the thecosomatous pteropod *Spiratella* (''*Limacina*'') *helicina* in the central Arctic Ocean. *Marine Biology*, 26, 295-301

Komar P.D., Morse A.P., Small L.F., Fowler S.W. 1981. An analysis of sinking rates of natural copepod and euphausiid faecal pellets. *Limnology and Oceanography*, 26, 172-180

Koppelmann R., Weikert H., Halsband-Lenk C., Jennerjahn T.C. 2004. Mesozooplankton community respiration and its relation to particle flux in the oligotrophic eastern Mediterranean. *Global Biogeochemical Cycles,* 18, GB1039, doi:10.1029/2003GB002121

Kosobokova K.N., Hopcroft R.R. 2010. Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin. *Deep-Sea Research II,* 57, 96-110

Kroeker K.J., Micheli F., Gambi M.C., Martz T.R. 2011. Divergent ecosystem responses within a benthic marine community to ocean acidification. *PNAS,* 108, 35: 14515-14520

Lalli C.M. 1970. Structure and function of the buccal apparatus of Clione limacina (Phipps) with a review of feeding in gymnosomatous pteropods. *Journal Experimental Marine Biolology and Ecology*, 4, 101–118

Lalli C.M., Gilmer R.W. 1989. Pelagic snails: The Biology of Holoplanktonic Gastropod Molluscs. Stanford, Stanford University Press

Lampert W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology*, 3, 21-27

Larson R. J. 1986. Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. *Journal of Experimental Marine Biology and Ecology*, 99, 2:107–120, doi:10.1016/0022-0981(86)90231-5

Laubscher R.K., Perissinotto R., Mcquaid C.D., 1993. Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biology* 13, 471-481

Le Quéré C., Harrison S.P., Prentice C., Buitenhuis E.T, Aumonts O., Bopp L., Claustre H., da Cunha L.C., Geider R., Giraud X., Klaas C., Kohfeld K.E., Legendre L., Manizza M., Plattss T., Rivkin R., Sathyendranath S., Uitz J., Watson A.J., Wolf-Gladrow, D. 2005 Ecosystem dynamics based on plankton functional types for global ocean biochemistry models. *Global Change Biology,* 11, 2016-2040

Le Quéré C., Sathyendranath S., Meike V., Buitenhuis E.T., Bopp L., Doney S., Dutkiewicz S., Geider R.J., Harrison S., Klaas C., Legendre L., Pesant S., Platt T., Prentice C., Rivkin R., Wolf-Gladrow D., Yamanaka Y. 2009. Observational needs of Dynamic Green Ocean Models, Proceedings of OceanObs'09: Sustained Ocean Observations and Information for Society (Vol. 2). Venice Italy, 21-25 September 2009, Hall J., Harrison D.E. & Stammer D., Eds., ESA Publication WPP-306, doi: 10.5270/OceanObs09.cwp.56

Lea D.W., Martin P.A., Chan D.A, Spero H.J. 1995. Calcium uptake and calcification rate in the planktonic foraminifer *Orbulina universa*. *Journal of Foraminiferal Research, 25, 14-25*

Leblanc K., Arístegui J., Armand L., Assmy P., Beker B., Bode A., Breton E., Cornet V., Gibson J., Gosselin M.-P., Kopczynska E., Marshall H., Peloquin J., Piontkovski S., Poulton A. J., Quéguiner B., Schiebel R., Shipe R., Stefels J., van Leeuwe M. A., Varela M., Widdicombe C., and Yallop M. 2012. A global diatom database – abundance, biovolume and biomass in the world ocean. *Earth Systems Science Data*, 4, 47-73, doi:10.5194/essd-4-47-2012

Lebrato M., Iglesias-Rodriguez D., Feely R.A., Greely D., Jones D.O.B., Suarez-Boche N., Lampitt R.S., Cartes J.E., Green D.R.H., Alker B. 2010. Global contribution of

echinoderms to the marine carbon cycle: $CaCO_3$ budget and benthic compartments. *Ecological Monographs,* 80, 3: 441-467

Lee K. 2001. Global net community production estimated from the annual cycle of surface water total dissolved inorganic carbon. *Limnology and Oceanography*, 46, 1287-1297

Legendre L., Le Fèvre J. 1992. Interaction between hydrodynamics and pelagic ecosystems: relevance to resource exploitation and climate change. *South African Journal of Marine Science*, 12, 477-486

Levitus S., Antonov J., Boyer T. 2005. Warming of the world ocean, 1955-2003. *Geophysical Research Letters*, 32, L02604, doi: 10.1029/2004GL021592

Lischka S., Büdenbender J., Boxhammer T., Riebesell U. 2011. Impact of ocean acidification and elevated temperatures on early juveniles of the polar shelled pteropod *Limacina helicina*: mortality, shell degradation, and shell growth. *Biogeosciences*, 8, 919-932

Little W. S., Copley N. J. 2003. WHOI Silhouette DIGITIZER, Version 1.0, Users Guide, WHOI Technical Report, Woods Hole Oceanographic Institution, WHOI Technical Report

Luo Y.W., Doney S.C., Anderson L.A., Benavides M., Bode A., Bonnet S., Boström, Böttjer D., Capone D. G., Carpenter E. J., Chen Y. L., Church M. J., Dore J. E., Falcón L. I., Fernández A., Foster R. A., Furuya K., Gómez F., Gundersen K., Hynes A. M., Karl D. M., Kitajima S., Langlois R. J., LaRoche J., Letelier R. M., Marañón E., McGillicuddy Jr. D. J., Moisander P. H., Moore C. M., Mouriño-Carballido B., Mulholland M. R., Needoba J. A., Orcutt K. M., Poulton A. J., Rahav E., Raimbault P., Rees A. P., Riemann L., Shiozaki T., Subramaniam A., Tyrrell T., Turk-Kubo K. A., Varela M., Villareal T. A., Webb E. A., White A. E., Wu J., Zehr J. P. 2012. Database of diazotrophs in global ocean: abundances, biomass and nitrogen fixation rates. *Earth Systems Science Data,* 4, 149-165, doi:10.5194/essd-4-149-2012

Lyman J.M., Good S.A., Gouretski V.V., Ishii M., Johnson G.C., Palmer M.D., Smith D.M., Willis J.K. 2010. Robust warming of the global upper ocean. *Nature, Letters*, 465, 334-337, doi: 10.1038/nature09043

Maas A.E., Elder L.E., Dierssen H.M., Seibel B.A. 2011. Metabolic response of Antarctic pteropods (Mollusca: Gastropoda) to food deprivation and regional productivity. *Marine Ecology Progress Series*, 441, 129-139

Maas A.E., Wishner K.F., Seibel B.A. 2012a. The metabolic response of pteropods to acidification reflects natural CO_2-exposure in oxygen minimum zones. *Biogeosciences*, 9, 747-757

Maas A.E., Wishner K.F., Seibel B.A. 2012b. Metabolic suppresion in the thecosomeatous pteropods as an effect of low temperature and hypoxia in the eastern tropical North Pacific, *Marine Biology*, 159, 1955-1967

Mackas D.L. and Galbraith M.D. 2002. Zooplankton Distribution and Dymnamics in North Pacific Eddy of Coastal Origin: I. Transport and Loss of Continental Margin Species. *Journal of Oceanography*, 58, 725-738

Manno C., Tirelli V., Accornero A., Fonda Umani S. 2010. Importance of the *Limacina helicina* faecal pellets contribution to the carbon pump, (Terra Nova Bay, Antarctica). *Journal of Plankton Research*, 32, 2: 145-152

Marañón E., Cermeño P., Latasa M., Tadonléké R.D., 2012. Temperature, resources, and phytoplankton size structure in the ocean. *Limnology and oceanography*, 57, 1266-1278, doi: 10.4319/lo.2012.57.5.1266

MAREMIP – MARine Ecosystem Model Intercomparison Project. http://lgmacweb.env.uea.ac.uk/maremip/index.shtml. (accessed 2012)

Marine Species Identification Portal. http://species-identification.org/ (accessed 2012/13).

Marrari M., Daly K.L., Timonin A., Semenova T. 2011. The zooplankton of Marguerite Bay, Western Antarctic Peninsula - Part I: Abundance, distribution, and population response to variability in environmental conditions. *Deep-Sea Research II*, 58, 1599-1613, doi:10.1016/j.dsr2.2010.12.007

Martinez E., Antoine D., D'Ortenzio F., Gentili B. 2009. Climate-Driven Basin_scale Decadal Oscillation of Oceanic Phytoplankton. *Science,* 326, 1253, doi: 10.1126/science.1177012

Matear R.J., Hirst A.C. 2003. Long-term changes in dissolved oxygen concentrations in the ocean caused by protracted global warming. *Global Biogeochemistry Cycles,* 17, 1125, doi:10.1029/2002GB001997

Matear R.J., Hirst A.C., McNeil B.I. 2000. Changes in dissolved oxygen in the Southern Ocean with climate change. *Geochemistry Geophysics Geosystems,* 1, 11*:* 1050-162, doi:10.1029/2000GC000086

Matson P.G., Martz T.R., Hofmann G.E. 2011. High-frequency observation of pH under Antarctic sea ice in the southern Ross Sea. *Antarcticc Science Ltd*, 1-7, doi:10.1017/S0954102011000551

Mazzocchi M.G., Christou E., Rastaman N., Siokou-Frangou I. 1997. Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean): I. General aspects, Oceanologica Acta, 20, 3: 521-535

McNeil B.I., Matear R.J. 2008. Southern Ocean acidification: A tipping point at 450-pp, atmospheric CO_2. *PNAS,* 105, 48: 18860-18864

Mileikovsky S.A. 1970. Breeding and larval distribution of the pteropod Clione limacina in the North Atlantic, Subarctic and North Pacific Oceans. *Marine Biology*, 6, 317-332

Moore J.K., Doney S.C., Lindsay K. 2004. Upper ocean ecosystem dynamics and iron cycling in a global three dimensional model. *Global Biogeochemical Cycles*, 18, GB4029

Morán X.A.G., Lopez-Urrutia A., Calvo- Díazi A., Li W.K.W. 2010. Increasing Importance of small phytoplankton in warmer ocean. Global Change Biology, 16, 3: 1137-1144, 10.1111/j.1365-2486.2009.01960.x

Moraitou-Apostolopoulou M., Zervoudaki S., Kapiris K. 2008. Mesozooplankton abundance in waters of the Aegean Sea; Hellenic Center of Marine Research, Institut of Oceanography, Hydrodynamics and Biogeochemical Fluxes in the Straits of the Cretan Arc (project), Greece

Moriarty R., Buitenhuis E.T., Le Quéré C., Gosselin M.-P. 2012. Distribution of known macrozooplankton abundance and biomass in the global ocean. *Earth Systems Science Data (Open Access Discussions), 5, 187-220*

Moriarty R., O'Brien T.D. 2012. Distribution of mesozooplankton biomass in the global ocean. *Earth System Science Data Discussions,* 5, 893-919, doi: 10.5194/essdd-5-893-2012

Mousseau L., Fortier L., Legendre L. 1998. Annual production of fish larvae and their prey in relation to size-fractioned primary production (Scotian Shelf, NW Atlantic). *ICES Journal of Marine Science,* 55, 44-57

Mucci A. 1983. The solubility of calcite and aragonite in seawater at various salinities, temperatures and 1 atmosphere total pressure. American Journal of Acience. 238, 780-799

National oceanographic Data Centre (NODC) – World Ocean Database (WOD), National Oceanic and Atmospheric Administration (NOAA), United States Department of Commerce. http://www.nodc.noaa.gov/OC5/SELECT/dbsearch/dbsearch.html (accessed 2011/12/13)

Nishikawa J., Matsuura H., Castillo L.V., Wilfredo L.C., Nishida S. 2007. Biomass, vertical distribution and community structure of mesozooplankton in the Sulu Sea and its adjacent waters. *Deep-Sea Research II,* 54, 114-130, doi:10.1016/j.dsr2.2006.09.005

NMFS-COPEPOD: The Global Plankton Database, NMFS-ST *Marine Ecosystems Division*, developed and led by Todd D. O'Brien, NOAA - National Oceanic and Atmospheric Administration, U.S. Department of Commerce. http://www.st.nfms.noaa.gov/plankton/ (accessed 2011/12)

Noji T.T., Bathmann U.V., von Bodungen B., Voss M., Antia A., Krumbholz M., Klein B., Peeken I., Noji C.I.-M., Rey F. 1997. Clearance of picoplankton-sized particles and formation of rapidly sinking aggregates by the pteropods, *Limacina retroversa. Journal of Plankton Research,* 19, 7: 863-875

O'Brien C.J., Peloquin J.A., Vogt M., Heinle M. Gruber N., Ajani P., Andruleit H., Aristegui J. et al. 2012. Global marine plankton functional type biomass distributions: coccolithophores. *Earth Systems Science Data (Open Access Discussions), 5, 491-520*

Ohman M.D. 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecological Monographs,* 60, 3: 257-281

Ono T., Midorikawa T., Watanabe Y.W., Tadokoro K., Saino T. 2001. Temporal increases of phosphate and apparent oxygen utilization in the subsurface waters of western subarctic Pacific from 1968 to 1998. *Geophysical Research Letters,* 28, 3285–88, doi:10.1029/2001GL012948

Orr C.J., Fabry V.J., Aumont O., Bopp. L., Doney S.C., Feely R.A., Gnanadesikan A., Gruber N., Ishida A., Joos F., Key R.M., Lindsay K., Maier-Reimer E., Matear R., Monfray P., Mouchet A., Najjar R.G., Plattner G.-K., Rodgers K.B., Sabine C.L., Sarmiento J.L., Schlitzer, R., Slater R.D., Totterdell I.J., Weirig M.-F., Yamanaka Y., Yool A. 2005. Anthropogenic ocean acidification over twenty-first century and its impact on calcifying organisms. *Nature*, 437

Pakhomov E.A., Perissinotto R., McQuaid C.D., 1996. Prey composition and daily rations of myctophid fishes in the Southern Ocean*. Marine Ecology Progress Series*, 134, 1–14

Pakhomov E.A., Perissinotto R. 1997. Mesozooplankton community structure and grazing impact in the region of the Subtropical Convergence south of Africa. *Journal of Plankton Research,* 19, 6: 675-691

Pakhomov E.A., Froneman P.W. 2004. Zooplankton dynamics in the eastern Atlantic sector of the Southern Ocean during the austral summer 1997/1998-Part 2: Grazing impact. *Deep-Sea Research II*, 51, 2617-2631

Pane L., Feletti, M., Francomacaro B., Mariottini G.L. 2004. Summer coastal zooplankton biomass and copepod community structure near Italian Terra Nova Base (Terra Nova Bay, Ross Sea, Antarctica). *Journal of Plankton Research*, 26, 12: 1479-1488

PANGAEA World Data Centre. http://www.pangaea.de/search?&q=maredat (accessed 2011/12/13).

Parmesan C., Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37-42

Perissinotto R. 1992. Mesozooplankton size-selektivity and grazing impact on the phytoplankton community of the Prince Edward Archipelago (Southern Ocean). *Marine Ecology Progress Series*, 79:243-258

Perissinotto R., McQuaid C.D. 1992. Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean archipelago. *Marine Ecology Progress Series,* 80, 15-27

Phelger C.F., Nelson M.M., Mooney B., Nichols P.D. 1999. Lipids of abducted Antarctic pteropod, Spongiobranchaea australis, and their hyperiid amphipod host. *Comparative Biochemistry and Physiology – Part B: Biochemistry and Molecular Biology*, 124, 295-307

Pinsonneault A.J., Matthews H.D., Galbraith E.D., Schmittner A. 2012. Calcium carbonate production response to the future ocean warming and acidification. *Biogeosciences*, 9, 2351-2364, doi: 10.5194/bg-9-2351-2012

Plattner G.K., Joos F., Stocker T.F., Marchal O. 2001. Feedback mechanisms and sensitivities of ocean carbon uptake under global warming. *Tellus Series B-Chemical and Physical Meteorology,* 53, 5, 564–92, doi: 10.1034/j.1600-0889.2001.530504.x

Pörtner H.-O. 2001. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften*, 88, 137-146, doi: 10.1007/s001140100216

Pörtner H.-O. 2002. Review. Physiological basis of temperature-dependent biogeography: trade-offs in muscle design and performance in polar ectotherms. *The Journal of Experimental Biology*, 205, 2217-2230

Pörtner H.-O. 2008. Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. *Marine Ecology Progress Series,* 373, 203-217, doi: 10.3354/meps07768

Pörtner H.-O, Peck L., Somero G. 2007. Thermal limits and adaptation in marine Antarctic ectorherms: an integrative view. *Phylosophycal Transactions of the Royal Society,* 362, 2233-2258, 10.1098/rstb.2006.1947

Pörtner H.O., Farrell A.P. 2008. Ecology: Physiology and climate change. *Science,* 322, 690–92

Pörtner, H.-O. 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology,* 213, 881–893, doi:10.1242/jeb.0375523

Ramfos A., Isari S., Rastaman N. 2008. Mesozooplankton abundance in water of the Ionian Sea (March 2000). Department of Biology, University of Patras

Raven J., Caldeira K., Elderfield H., Hoegh-Guldberg O., Liss P., Riebesell U., Shepherd J. Turley C., Watson A. 2005. Ocean acidification due to increasing atmospheric carbon dioxide.*The Royal Society*, a policy document, London, UK

Redfield A.C. 1939. The history of population of *Limacina retroversa* during its drift across the Gulf of Maine. *Biological Bulletin*, 76 (1)

Richardson A.J., Schoeman D.S. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, 305, 1609-16012

Riebsell U., Fabry V.J., Hansson L., Gattuso J.-P. (Eds.) 2010. Guide to best practices for ocean acidification research and data reporting, 260 p. Luxemburg: Publications Office of the European Union

Rivkin R. B., Legendre L. 2001. Biogenic carbon cycling in the upper ocean: Effects of microbial respiration. *Science*, 291, 2398–2400, doi:10.1126/science.291.5512.2398

Rogachev K.A., Carmack E.C., Foreman M.G.G. 2008. Bowhead whales feed on plankton concentrated by estuarine and tidal currents in Academy Bay, Sea of Okhotsk. *Continental Shelf Research,* 28, 1811-1826, doi:10.1016/j.csr.2008.04.014

Rosenthal J.J.C, Seibel B.A., Dymowska A., Bezanilla. 2012. Trade-off between aerobic capacity and locomotors capability in an Antarctic pteropod. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 15: 6192-6196

Sabine C. L., Feely R. A., Gruber N., Key R. M., Lee K., Bullister J. L., Wanninkhof R., Wong C. S., Wallace D. W. R.., Tilbrook B, Millero F. J., Peng T. H., Kozyr A., Ono T.,

Rios A. F. 2004. The oceanic sink for anthropogenic CO_2. *Science,* 305, 367–371, doi:10.1126/science.1097403

Sabine C.L., Feely R.A. 2007. The Oceanic Sink for Carbon Dioxide. Greenhouse Gas Sinks, Reay D., Hewitt N., Grace J., Smith K. (Eds.), CABI, Oxfordshire, UK

Sakshaug E. 2003. Primary and secondary production in the Arctic seas. In: Stein R., Macdonald R.W. (Eds.). The organic carbon cycle in the Arctic Ocean. Springer, Berlin Heidelberg New York: pp. 57-81

Sarmiento J.L., Gruber N. 2004. Ocean Biogeochemical Dynamics, Chapter 10: Oceanic carbon cycle, atmospheric CO_2, and climate. *Princeton University Press,* September 10

Sarmiento J.L., Gruber N., Brzezinski M.A., Dunne J.P. 2004. High-latitude controls of thermocline nutrients and low latitude biological productivity. *Nature,* 427, 56–60

Sarmiento J.L., Dunne J., Ganandesikan A., Key R., Matsumoto K., Slater R. 2002. A new estimated of the $CaCO_3$ to organic carbon export ration. *Global Biogeochemical Cycles*, 16, 1107, doi: 10.1029/2002GB001919

Sato-Okoshi W., Okoshi K., Sasaki H., Akiha F. 2010. Shell structure of two polar pelagic molluscs, Arctic *Limacina helicina* and Antarctic *Limacina helicina antarctica. Polar Biology,* 33, 1577-1583

Schalk, P. H. 1990. Spatial and seasonal variation in pteropods (Mollusca) of Indo-Malayan waters related to watermass distribution. *Marine Biology*, 105, 59-71

Schiebel R. 2002. Planktic foraminiferal sedimentation and the marine calcite budget. *Global Boogeochemical Cycles,* 16, 13-21

Schiebel R., Movellan A. 2012. First-order estimate of the planktic foraminider biomass in the modern global oceans. *Earth Systems Science Data,* 4, 75-89, doi:10.5194/essd-4-75-2012

Schnack-Schiel S. B., Cornils A. 2009. Zooplankton abundance measured on Apstein net samples during cruise CISKA2005. Alfred Wegener Institute for Polar and Marine Research, Science for the Protection of Indonesian Coastal Environment (project), Bremerhaven

Seibel B.A. 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *The Journal of Experimental Biology*, 214, 326-336

Seibel B.A., Dierssen H.M. 2003. Cascading trophic impacts of reduced biomass in the Ross Sea Antarctica: just the tip of the iceberg?. *Biological Bulletin,* 205, 93–97

Seibel B.A., Dierssen H. M. 2009. Perspective: animal function at the heart (and gut) of oceanography. *Science*, 323, 343-344

Seibel B.A., Dymowska A., Rosenthal J. 2007. Metabolic temperature compensation and coevolution of locomotory performance in pteropod molluscs, *Integrative and Comparative Biology*, 47, 6: 880-891

Seibel B.A., Maas A.E., Dierssen H.M. 2012. Energetic Plasticity Underlies a Variable Response to Ocean Acidification in the Pteropod, *Limacina helicina antarctica*. *PLoS ONE* 7, 4: e30464

Silverman J., Lazar B., Erez J. 2007. Effect of aragonite saturation, temperature and nutrients on the community calcification rate of coral reef. *Journal of Geophysical Research*, 112, C05004, doi:10.1029/2006JC003770

Siokou-Frangou I., Christou E., Rastman N. 2008. Mesozooplankton abundance in waters of the Ionian Sea. Hellenic Center of Marine Research, Institut of Oceanography, Physical Oceanography of the Eastern Mediterranean (project), Greece

Swadling K.M., Penot F., Vallet C., Rouyer A., Gasparini S. 2011. Mousseau, L. and Smith, M. and Goffart, A., Interannual variability of zooplankton in the Dumont d'Urville sea (139 °E- 146 °E) , east Antarctica, 2004-2008. *Polar Science*, 5, 118-133, doi:10.1016/j.polar.2011.03.001

Smith K.L. Jr., Teal J.M. 1973. Temperature and pressure effects on respiration of thecosomatous pteropods. *Deep-Sea Research*, 20, 853-858

Solis N.B., von Westernhagen H. 1978. Vertical distribution of Euthecosomatous Pteropods in the upper 100 m of the Hilutangen Channel, Cebu, The Philippines. *Marine Biology,* 48, 79-87

Spalding M.D., Fox H.E., Allen G.R., Davidson N., Ferdana Z.A., Finlayson M., Halpern B.S., Jorge M.A., Lombana A., Lourie S.A., Martin K.D., McManus E., Molnar J., Recchia C.A., Robertson J. 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*, 57, 7

Steinacher M., Joos F., Frölicher T. L., Plattner G., Doney S. C. 2009. Imminent ocean acidification in the Arctic projected with the NCAR global coupled carbon cycle-climate model. *Biogeosciences*, 6, 515–533, doi:10.5194/bg-6-515-2009

Stepien J.C. 1980. The occurrence of chaetognaths, pteropod and euphasiids in relation to deep flow recersals in the Straits of Florida. *Deep-Sea Research*, 27A, 987-1011

Storey K.B., Tanino K.K. (Eds.). 2012. Temperature Adaptation in a Changing Climate: Nature at Risk. Abele D. Chapter 5: Temperature Adaptation in Changing Climate: Marine Fish and Invertebrates. CABI: pp. 67-79

Stramma L., Johnson G. C., Sprintall J., Mohrholz V. 2008. Expanding oxygen-minimum zones in the tropical oceans. *Science*, 320, 655-658

Taghon G.L., Nowell A.R.M., Jumars P.A., 1984. Transport and breakdown of faecal pellets: biological and sedimentological consequences. *Limnology and Oceanography*, 29, 64-71

Taylor J.R. 1996. An Introduction to Error Analysis: The Study of Uncertanties in Physical Measurements. University Science Books, 2nd edition (August 1, 1996): pp. 166-167

Tortell P.D., Payne C.D., Li Y., Trimborn S., Rost B., Smith W.O., Riesselman C., Dunbar R.B., Sedwick P., DiTullio G.R. 2008. CO_2 sensitivity of Southern Ocean phytoplankton. *Geophysical Research Letters*, 35, L04605, 5, doi:10.1029/2007GL032583

Tsurumi M., Mackas D.L., Whitney F.A., DiBacco C., Galbraith M.D., Wong C.S. 2005. Pteropods, eddies, carbon flux and climate variability in Alaska Gyre. *Deep-Sea Research II*, 52, 1037-1053

Van der Spoel, S. 1967. Euthecosomata: A Group with Remarkable Developmental Stages (Gastropoda, Pteropoda). J. Noorduijn en Zoon N.V., the University of California*:* pp. 1-375

Van der Spoel S. 1970. Morphometric data on Cavolinidae, with notes on a new form of *Cuvierina columnella* (Rang 1827) (Gastropoda, Pteropoda). Basteria, 34, (5, 6): 103-151

Van der Spoel S. 1973. Growth, reproduction and vertical migration in *Clio pyramidata* Linne, 1767 forma *lunceolata* (Lesueur, 1813), with notes on some other Cavoliniidae (Mollusca, Pteropoda). *Beaufortia,* 281*,* 117-134

Van der Spoel S. 1976. Pseudothecosomata, Gymnosomata, and Heteropoda (Gastropoda). Bohn, Scheltema & Holkema, Utrecht, 484 pp.

Van der Spoel S., Dadon J.R., 1999. Pteropoda. In: Boltovsky D. (Ed.): South Atlantic Zooplankton. Bachuys Publishers, Leide, Netherlands, pp. 649-706

Vogt M., O'Brien C., Pelquin J., Schoemann V., Breton E., Estrada M., Gibson J., Karentz D., Van Leeuwe M.A., Stefels J., Widdicombe C., Peperzak L. Global marine plankton type biomass distributions: Pheocystis sp.. *Earth Systems Science Data*, 4, 107-120, doi:10.5194/essd-4-107-2012

Volkov A.F. 2008. Integral Patterns of Quantative Distribution of Mass Zooplankton Species in Far Eastern Seas and the North-Western Pacific Ocean Basing on the Annual Mean Data of 1984-2006. *Russian Journal of Marine Biology*, 34, 7: 490-496

Ward P., Whitehouse M., Brandon M., Shreeve R., Woodd-Walker R. 2003. Mesozooplankton community structure across the Antarctic Circumpolar Current to the north of South Georgia: Southern Ocean. *Marine Biology,* 143, 121–130

Ward P., Whitehouse M., Shreeve R., Thorpe S., Atkinson A., Korb R., Pond D., Young E. 2007. Plankton community structure south and west of South Georgia (Southern Ocean): Links with production and physical forcing. *Deep-Sea Research I,* 54, 1871-1889, doi:10.1016/j.dsr.2007.08.008

Wells F.E. Jr. 1973. Effects of Mesh Size on Estimation of Population Densities of Tropical Euthecosomatous Pteropods. *Marine Biology*, 20, 347-350

Wells F.E. 1976. Seasonal patterns of abundance and reproduction of euthecosomatous pteropods off Barbados, West Indies. *Veliger*, 18, 241-248

Werner I. 2005. Living conditions, abundance and biomass of under-ice fauna in the Storfjord area (Western Barents Sea, Arctic) in late winter (March 2003). *Polar Biology*, 28, 311-318

Whitney F.A., Freeland H.J., Robert M. 2007. Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. *Progress in Oceanography,* 75, 179–99

Widdicombe S., Spicer J.I. 2008. Predicting the impact of ocean acidification on benthic biodiversity: What can animal physiology tell us?. *Journal of Experimental Marine Biology and Ecology,* 366, 1-2: 187-197

Williamson C.E., Fischer J.M., Bollens S.M., Overholt E.P., Breckenridge J.K. 2011. Toward a more comprehensive theory of zooplankton vertical migration: Itergating ultravioler radiation adn water transparency into biotic paradigm. *Limnology and Oceanography*, 56, 5: 1603-1623, doi: 10.4319/lo.2011.56.5.1603

Wilson R.W., Millero F.J., Taylor J.R., Walsh P.J., Christensen V., Jennings S., Grosell M. 2009. Contribution of fish to the marine inorganic carbon cycle. *Science*, 323, 359-362

Wood H.L., Spicer J.I., Widdicombe S. 2008. Ocean acidification may increase calcification rates, but at a cost. *Procedings of Biological Sciences*, 275, 1767–1773

Wormuth J.H. 1981. Vertical distributions and diel migrations of Euthecosomata in the northwest Sargasso Sea. *Deep Sea Research Part A*, *Oceanographic Research Papers*, 28, 12: 1493-1515

Wormuth J. H. 1985. The role of cold-core Gulf Stream rings in the temporal and spatial patterns of euthecosomatous pteropods. *Deep-Sea Res*earch, 32, 773–788

Yamamoto-Kawai M., McLaughlin F. A., Carmack E. C., Nishino S., Shimada K. 2009. Aragonite undersaturation in the Arctic Ocean: effects of ocean acidification and sea ice melt. *Science*, 326, 1098–1100, doi:10.1126/science.1174190

Yin J., Overpeck J.T., Griffies S.M. , Hu A., Russell J.L., Stouffer R.J. 2011. Different magnitudes of projected subsurface ocean warming around Greenland and Antarctica. *Nature Geoscience, Letters*, advance online publication, doi: 10.1038/NGEO1189

Yoon W., Kim S., Han K. 2001. Morphology and sinking velocities of faecal pellets of copepod, molluscan, euphausiid, and salp taxa in the northeastern tropical Atlantic. *Marine Biology,* 139, 923-928

Zervoudaki S., Christou E., Siokou-Frangou I., Zoulias T. 2008. Mesozooplankton abundance in water of the Aegean Sea,; Hellenic Center of Marine Research, Institut of Oceanography, Greece

ZooDB – Zooplankton database, Plankton sample analysis supported by NSF grants to M.D. Ohman, Scripps Institution of Oceanography and by the SIO Pelagic Invertebrates Collection. http://oceaninformatics.ucsd.edu/zoodb/# (accessed 2011/12)

ANNEX A

Lengths of pteropods used in length-to-weight conversion equations (Marine Species Identification Portal, 2012)

Order	Suborder	Taxon	Subspecies /Formae	Mean shell length [mm]	Mean shell width [mm]	Body length [mm]	Shell/ body shape	Additional information	Group
Thecosomata	Euthecosomata	*Limacina helicina*	*helicina helicina*	6	8		round	left coiled shell, moderately highly spired, aperture higher than wide, height/diameter ration=0,75	Round/cylindrical/globular
Thecosomata	Euthecosomata	*Limacina helicina*	*helicina pacifica*	5	2				Round/cylindrical/globular
Thecosomata	Euthecosomata	*Limacina retroversa*	*retroversa*	2,5	2,6		round	small, left coiled shell, no umbilical keel, spire moderately highly coiled	Round/cylindrical/globular
Thecosomata	Euthecosomata	*Limacina bulimoides*		2	1,4		round	highly coiled spire	Round/cylindrical/globular
Thecosomata	Euthecosomata	*Limacina inflata*			1,3		round	coiled nearly in one level; shell diameter=0,86, aperture length=0,68 mm, diameter of operculum=0,31mm, aperture breadth=0,5 mm (average sized specimen!)	Round/cylindrical/globular
Thecosomata	Euthecosomata	*Limacina helicina*	*antartica antarctica*		5		round	left coiled, spire variable	Round/cylindrical/globular
Thecosomata	Euthecosomata	*Limacina helicina*	*antartica antarctica rangi*	2	3,5				Round/cylindrical/globular
Thecosomata	Euthecosomata	*Limacina trochiformis*		1	0,8		round	left coiled, apical angle 75-96°	Round/cylindrical/globular
Thecosomata	Euthecosomata	*Limacina helicina spp. average*			4,22				Round/cylindrical/globular

It continues.

Continuing.

Order	**Suborder**	**Taxon**	**Subspecies /Formae**	**Mean shell length [mm]**	**Mean shell width [mm]**	**Body length [mm]**	**Shell/ body shape**	**Additional information**	**Group**
Thecosomata	Euthecosomata	*Limacina trochiformis*		1	0,8		round	left coiled, apical angle 75-96°	Round/cylindrical/globular
Thecosomata	Euthecosomata	*Limacina lesueuri*		0,8	1		round	flatly left coiled, spire depressed; max diameter of operculum=0,6 mm and length/width ratio=2/3	Round/cylindrical/globular
Thecosomata	**Euthecosomata**	***Limacina spp.***			**2,98**			**calculated as the average of all species**	**Round/cylindrical/globular**
Gymnosomata		*Clione limacina*	*limacina antarctica*		25	Up to 40	barell	body pointed posteriorly	Barrel/oval-shaped (naked)
Gymnosomata		*Clione limacina*	*limacina meridionalis*		21	20	barell	cone elongated	Barrel/oval-shaped (naked)
Gymnosomata					12				
Gymnosomata		*Clione limacina larvae*			0,3				
Gymnosomata		***Clione spp.***			**14,575**			**calculated as the average of all species**	**Barrel/oval-shaped (naked)**
Thecosomata	**Euthecosomata**	***Hyalocylis striata***		**8**		**up to 8**	**cylindrical**	**uncoiled, cross-section round, shell curved faintly dorsally; rear angle of adult shell 24°**	**Cone-shaped (needle/tube/bottle)**
Thecosomata	**Euthecosomata**	***Styliola subula***		**13**		**13**	**needle-like**	**shell is (conical), uncoiled, the cross-section is round, long, tubular, not curved; rear angle of shell is 11°**	**Cone-shaped (needle/tube/bottle)**

It continues.

Continuing.

Order	**Suborder**	**Taxon**	**Subspecies /Formae**	**Mean shell length [mm]**	**Mean shell width [mm]**	**Body length [mm]**	**Shell/ body shape**	**Additional information**	**Group**
Gymnosomata		*Spongiobranchaea australis*		20		max 22	oval	long body	Barrel/oval-shaped (naked)
Gymnosomata		*Spongiobrachaea australis juv.*		10					Barrel/oval-shaped (naked)
Gymnosomata		***Spongiobranchaea spp.***		**15**					**Barrel/oval-shaped (naked)**
Gymnosomata		*Pneumodermopsis*	*teschi*			up to 9,1	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*pulex*			up to 8	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*macrochira*			up to 2	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*ciliata*			up to 15	barrel	slender body	Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*spoeli*			up to 3 (2,6)	barrel	body rounded then contracted	Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*simplex*			up to 5 (4,5)	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*paucidens*			up to 5	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*canephora*			up to 12	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*polycotyla*			up to 5	barrel		Barrel/oval-shaped (naked)

It continues.

Continuing.

Order	**Suborder**	**Taxon**	**Subspecies /Formae**	**Mean shell length [mm]**	**Mean shell width [mm]**	**Body length [mm]**	**Shell/ body shape**	**Additional information**	**Group**
Gymnosomata		***Pneumodermopsis spp.***				**6,51**		**calculated as the average of all species**	**Barrel/oval-shaped (naked)**
Gymnosomata		***Paedocline***	***doliiformis***	**1,5**				**elongate oval to cylindrical shape**	**Barrel/oval-shaped (naked**
Thecosomata	Euthecosomata	*Cavolinia globulosa*		6	4,5		globular		Triangular/ pyramidal
Thecosomata	Euthecosomata	*Cavolinia inflexa*	*inflexa*	7	5	6	triangular		Triangular/ pyramidal
Thecosomata	Euthecosomata	*Cavolinia inflexa*	*imitans*	8			triangular		Triangular/ pyramidal
Thecosomata	Euthecosomata	*Cavolinia inflexa*	*labiata*	8	5,5		triangular		Triangular/ pyramidal
Thecosomata	Euthecosomata	*Cavolinia longirostris*	*f. longirostris*	6,24	6.8-4.96	7	triangular	accepted name Dicavolinia longirostris!	Triangular/ pyramidal
Thecosomata	Euthecosomata	*Cavolinia longirostris*	*f. angulosa*	3,9	3.72-2.32	5	triangular	accepted name Dicavolinia longirostris!	Triangular/ pyramidal
Thecosomata	Euthecosomata	*Cavolinia longirostris*	*f. strangulata*	4	4.16-2.76	5	triangular	accepted name Dicavolinia longirostris!	Triangular/ pyramidal
Thecosomata	Euthecosomata	*Cavolinia uncinata*	*uncinata uncinata*	6,5	4,0-6,6	8	triangular	uncoiled shell	Triangular/ pyramidal
Thecosomata	Euthecosomata	*Cavolinia uncinata*	*uncinata f. pulsatapusilla*	6,1	9,5		triangular		Triangular/ pyramidal

It continues.

Continuing.

Order	Suborder	Taxon	Subspecies /Formae	Mean shell length [mm]	Mean shell width [mm]	Body length [mm]	Shell/ body shape	Additional information	Group
Thecosomata	**Euthecosomata**	***Cavolinia spp.***		**6,19**				**calculated as the average of all species**	**Triangular/ pyramidal**
Thecosomata	Euthecosomata	*Clio convexa*		8	4,5	up to 8	pyramidal	shell uncoiled	Triangular/ pyramidal
Thecosomata	Euthecosomata	*Clio cuspidata*		20	30	up to 20	pyramidal	shell uncoiled	Triangular/ pyramidal
Thecosomata	Euthecosomata	*Clio piatkowskii*		13,5	16	14	broad pyramidal		Triangular/ pyramidal
Thecosomata	Euthecosomata	*Clio pyramidata*		20	10		pyramidal		Triangular/ pyramidal
Thecosomata	Euthecosomata	*Clio pyramidata*	*martensi*	17					Triangular/ pyramidal
Thecosomata	Euthecosomata	*Clio pyramidata*	*antarctica*	17					Triangular/ pyramidal
Thecosomata	Euthecosomata	*Clio pyramidata*	*lanceolata*	20					Triangular/ pyramidal
Thecosomata	Euthecosomata	*Clio pyramidata spp.*		18,5					Triangular/ pyramidal
Thecosomata	**Euthecosomata**	***Clio spp.***		**16,5**				**calculated as the average of all species**	**Triangular/ pyramidal**
Thecosomata	Euthecosomata	*Creseis acicula*	*acicula*	33	1,5		tube	shell is not curved, cross-section circular, extremely long and narrow, aperture rounded, rear angle of shell 13-14°	Cone-shaped (+needle/tube/bottle)

It continues.

Continuing.

Order	**Suborder**	**Taxon**	**Subspecies /Formae**	**Mean shell length [mm]**	**Mean shell width [mm]**	**Body length [mm]**	**Shell/ body shape**	**Additional information**	**Group**
Thecosomata	Euthecosomata	*Creseis acicula*	*clava*	6					Cone-shaped (+needle/tube/bottle)
Thecosomata	Euthecosomata	*Creseis acicula spp.*		19,5					Cone-shaped (+needle/tube/bottle)
Thecosomata	Euthecosomata	*Creseis virgula*	*virgula*	6	max 2	6	tube	shell is curved (distinctly curved dorsally), uncoiled, long and narrow	Cone-shaped (+needle/tube/bottle)
Thecosomata	Euthecosomata	*Creseis virgula*	*conica*	7	aperture-diameter=1 mm	up to 7	tube	shell curved and slender, cross-section is round	Cone-shaped (+needle/tube/bottle)
Thecosomata	Euthecosomata	*Creseis virgula*	*constricta*	3,5	0,38	4	tube	uncoiled shell, cross-section round, short and narrow, slightly curved	Cone-shaped (+needle/tube/bottle)
Thecosomata	Euthecosomata	*Creseis virgula spp.*		5,5	0,2		tube		Cone-shaped (+needle/tube/bottle)
Thecosomata	**Euthecosomata**	***Creseis spp.***		**11,5**					**Cone-shaped (+needle/tube/ bottle)**
Thecosomata	**Euthecosomata**	***Cuvierina columnella***	***columnella***	**10**	**3**	**up to 10**	**bottle-shaped**	**the greatest shell width is found at less than 173 of the shell length from posterior**	**Cone-shaped (+needle/tube/ bottle)**
Thecosomata	Euthecosomata	*Diacria costata*		2,25	1.72-2.24	3	globular	shell uncoiled	Triangular/ pyramidal

It continues.

Continuing.

Order	Suborder	Taxon	Subspecies /Formae	Mean shell length [mm]	Mean shell width [mm]	Body length [mm]	Shell/ body shape	Additional information	Group
Thecosomata	Euthecosomata	*Diacria danae*		1,75	1.1-1.7	2	globular	shell uncoiled	Triangular/ pyramidal
Thecosomata	Euthecosomata	*Diacria quadridentata*		3	1.84-2.48	2	globular	shell uncoiled	Triangular/ pyramidal
Thecosomata	Euthecosomata	*Diacria rampali*		9,5	9	9	cone-shaped	bilateral symmetrical, uncoiled shell, slender, long caudal spine; spine mark width=0,95 mm, aperture height= 0,95.	Triangular/ pyramidal
Thecosomata	Euthecosomata	*Diacria trispinosa*	*trispinosa*	8	10	1	cone-shaped	bilateral symmetrical, uncoiled shell, long caudal spine; the ration upperlip-spine tip/spine tip-membrane=1,3, spine mark width=1,5 mm, aperture height=0,9 mm.	Triangular/ pyramidal
Thecosomata	Euthecosomata	*Diacria major*		10,75	11			uncoiled bilateral symmetrical, long caudal spine; ratio upperlip-spine tip/spine-tip membrane= 1,65 mm, spine mark width= 1,2 mm, aperture height= 1 mm;	Triangular/ pyramidal
Thecosomata	**Euthecosomata**	***Diacria spp.***		**5,88**					**Triangular/ pyramidal**
THECOSOMATA SUMA				**8,11**				**shelled**	
GYMNO-SOMATA SUMA						**12,04**		**naked**	
PTEROPODA SUMA				**8,89**				**shelled**	

ANNEX B

B1) Respiration rate as a function of temperature

Reference	Order	Taxa	Temperature [°C]	n (nb. of experiments/specimen)	Wet Mass [mg]*	MO2 [µmol O2 g wet mass-1 h-1]; mass specific oxygen consumption rate	Oxygen consumption rate [g C g C-1 day-1]	SE (standard error)	Equation	Add. info	Temperature coefficients (Q10)	Notes
Seibel B.A. et al. (2007)	Thecosomata	*Limacina helicina*	-2	22	8.49	5.51	0.006348	0.44				Oxygen consumption rates (MO2. [µmol O2 g -1 h -1]) decline with wet body mass (M, [g]) according to the power equation, MO2=aMb, where a is a normalization constant independent of mass and temperature, and b is a scaling coefficient that describes the slope of the relationship. Temperature coefficients [Q10=(a1/a2)(10/(T2 T1)] were determined from the normalization constants measured at different temperatures. Normalization constants for C. antarctica at 2°C and 28°C are higher than are those of C. limacina at 10 °C and 58 °C, respectively, suggesting that temperature compensation of some energetically expensive physiological process is reflected in whole-animal metabolic rates.
Seibel B.A. et al. (2007)	Thecosomata	*Limacina helicina*	-2	12	8.25	3.79	0.004366	0.16		starved		
Seibel B.A. et al. (2007)	Thecosomata	*Limacina helicina*	5	10	3.2	6.37	0.007338	0.868				
Seibel B.A. et al. (2007)	Thecosomata	*Cavolinia tridentata*	18	3	50.5	10.99	0.01266	3.23				
Seibel B.A. et al. (2007)	Thecosomata	*Cavolinia tridentata*	24	2	6	17.25	0.019872					
Seibel B.A. et al. (2007)	Thecosomata	*Cavolinia tridentata*	24	2	11	17.23	0.019849					
Seibel B.A. et al. (2007)	Thecosomata	*Corolla spp.*	5	4	11305	0.226	0.00026	0.11				
Seibel B.A. et al. (2007)	Thecosomata	*Corolla spp.*	18	1	0.327	0.582	0.00067					
Seibel B.A. et al. (2007)	Gymnosomata	*Clione antarctica*	-2	31	140.4	2.04	0.00235	0.116	MO_2=0.84 M-0.29		3.6	
Seibel B.A. et al. (2007)	Gymnosomata	*Clione antarctica*	-2	30	70	0.99	0.00114	0.05	MO_2=0.84 M-0.29	starved	3.6	
Seibel B.A. et al. (2007)	Gymnosomata	*Clione antarctica*	2	20	123.8	2.83	0.00326	0.177	MO_2=1.50 M-0.23		3.6	

It continues.

Continuing.

Reference	Order	Taxa	Temperature [°C]	n (nb. of experiments/specimen)	Wet Mass [mg]*	MO2 [µmol O2 g wet mass-1 h-1]; mass specific oxygen consumption rate	Oxygen consumption rate [g C g C-1 day-1]	SE (standard error)	Equation	Add. info	Temperature coefficients (Q10)	Notes
Seibel B.A. et al. (2007)	Gymnosomata	*Clione limacina*	5	23	488.5	1.36	0.001567	0.155	MO_2=0.58 M-0.43		4.26	
Seibel B.A. et al. (2007)	Gymnosomata	*Clione limacina*	5	9	217	1.01	0.001164	0.09	MO_2=0.58 M-0.43	starved	4.26	
Seibel B.A. et al. (2007)	Gymnosomata	*Clione limacina*	10	20	343.5	1.95	0.002246	0.149	MO_2=1.1 M-0.31		4.26	
Seibel B.A. et al. (2007)	Gymnosomata	*Pneumodermopsis spp.*	18	2	256	3.99	0.004596					
Seibel B.A. et al. (2007)	Gymnosomata	*Pneumodermopsis spp.*	18	2	256	2.05	0.002362					
Seibel B.A. et al. (2007)	Gymnosomata	*Pneumodermopsis spp.*	24	2	5	40.94	0.047163					
Seibel B.A. et al. (2007)	Gymnosomata	*Cliopsis krohni*	5	3	789.5	0.06	6.91E-05	0.02				
Seibel B.A. et al. (2007)	Gymnosomata	*Cliopsis krohni*	5	4	1775	0.055	6.34E-05	0.014				
Seibel B.A. et al. (2007)	Gymnosomata	*Cliopsis krohni*	24	1	132	1.672	0.001926					
Seibel B.A. et al. (2007)	Gymnosomata	*Thliptodon spp.*	5	1	740	0.067	7.72E-05			deep		
Seibel B.A. et al. (2007)	Gymnosomata	*Thliptodon spp.*	20	1	56	0.693	0.000798					*some of the wet mass values were calculated from the given range of measured wet mass values as mean wet mass values.
Seibel B.A. et al. (2007)	Gymnosomata	*Notobranchia grandis*	5	1	910	0.1	0.000115			deep		

It continues.

Continuing.

Reference	Order	Taxa	Temperature [°C]	n	Mean chl-a [mg m-3]	Oxygen consumption rate [µmol O2 g-1 h-1]	Oxygen consumption rate [g C g C-1 day-1]	SE	Equation	Add. info	Notes
Seibel B.A. and Dierssen H.M., (2003)	Thecosomata	*Limacina helicina*	-1.86	12	3.9 (and 1.5)**	5.51	0.00634752	0.4			
Seibel B.A. and Dierssen H.M., (2003)	Thecosomata	*Limacina helicina*	-1.86	22	1.0 (and 2.2)**	3.78	0.00435456	0.2			
Seibel B.A. and Dierssen H.M., (2003)	Gymnosomata	*Clione antarctica*	-1.86	33		0.99	0.00114048	0.05	Oxygen consumption=0.4 (wet body mass)-0.28	food deprivation	**Chlorophyll measured twice (only relevant for Limacina helicina as a food source!); Table 1 (Seibel B.A. and Dierssen H.M., 2003)
Seibel B.A. and Dierssen H.M., (2003)	Gymnosomata	*Clione antarctica*	-1.86	31		2.04	0.00235008	0.12	Oxygen consumption=0.93 (wet body mass)-0.25		
Seibel B.A. and Dierssen H.M., (2003)	Gymnosomata	*Clione antarctica*	-1.86	10		1.93	0.00222336	0.21			
Seibel B.A. and Dierssen H.M., (2003)	Gymnosomata	*Clione antarctica*	-1.86	7		0.96	0.00110592	0.1		starved (lab experiment)	

It continues.

Continuing.

Reference	Order	Taxa	Temperature [°C]	n (nb. of experiments)	Ash-free dry weight [mg]	b	Seb (standard error of b)	a	Respiration rate [mm3 O2 mg-1 hr-1]	Oxygen consumption rate [g C g C-1 day-1]	Equation	Notes
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Diacria trispinosa*	0	13	4.15	-0.3789	0.1915	1.6516	0.079165	0.0040726		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Diacria trispinosa*	5	8	4.15	-0.3936	0.2779	2.4904	0.85696	0.0440855		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Diacria trispinosa*	10	42	4.15	-0.4034	0.1163	3.0381	1.36399	0.0701691		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Diacria trispinosa*	15	14	4.15	-0.3838	0.2705	3.7014	2.10863	0.1084764		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Diacria trispinosa*	20	17	4.15	-0.3973	0.313	4.3798	2.731005	0.1404938		Combined effects of pressure and temperature on respiration rate generally show increased respiration with increased pressure (Figure 2)!
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Diacria trispinosa*	25	34	4.15	-0.3818	0.1013	4.7627	3.17823	0.1635009		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Diacria trispinosa*	30	8	4.15	-0.3834	0.2161	5.1301	3.53899	0.1820598		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Cuvierina columnella*	10	6	3.4	-0.3739	0.2154	1.5223	0.25104	0.0129145		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Cuvierina columnella*	15	35	3.4	-0.3895	0.1224	2.2877	0.9634	0.0495611		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Cuvierina columnella*	20	88	3.4	-0.3976	0.0562	2.8642	1.51236	0.0778018	Y=bX+a (y=respiration [mm3 O2 mg-1 hr-1]; X=body weight [mg])	
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Cuvierina columnella*	25	54	3.4	-0.3816	0.0943	3.3264	2.02896	0.1043778		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Cuvierina columnella*	30	16	3.4	-0.3875	0.2258	3.8356	2.5181	0.1295411		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Clio pyramidata*	0	17	5.05	-0.3332	0.1294	1.6971	0.01444	0.0007429		

It continues.

Continuing.

Reference	Order	Taxa	Temperature [°C]	n (nb. of experiments)	Ash-free dry weight [mg]	b	Seb (standard error of b)	a	Respiration rate [mm3 O2 mg-1 hr-1]	Oxygen consumption rate [g C g C-1 day-1]	Equation	Notes
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Clio pyramidata*	5	48	5.05	-0.3486	0.1008	2.3124	0.55197	0.0283955		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Clio pyramidata*	10	28	5.05	-0.3405	0.1566	2.7271	1.007575	0.0518337		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Clio pyramidata*	15	25	5.05	-0.3422	0.1304	3.4361	1.70799	0.0878658		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Clio pyramidata*	20	30	5.05	-0.3332	0.1289	3.9971	2.31444	0.1190641		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Clio pyramidata*	25	11	5.05	-0.3344	0.1475	4.4632	2.77448	0.1427303		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Clio pyramidata*	30	8	5.05	-0.3329	0.2116	4.9231	3.241955	0.1667791		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Limacina helicoides*	0	16	1.4	-0.4395	0.0983	2.1319	1.5166	0.07802		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Limacina helicoides*	5	38	1.4	-0.4235	0.0621	2.3929	1.8	0.0925992		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Limacina helicoides*	10	23	1.4	-0.4326	0.0411	2.6516	2.04596	0.1052524		
Smith K.L. Jr. and Teal J.M. (1973)	Thecosomata	*Limacina helicoides*	15	4	1.4	-0.418	0.1456	3.8145	3.2293	0.1661281		

It continues.

Continuing.

Reference	Order	Taxa	Temperature [°C]	SD	n	b	SE ab	Equation	Notes
Biggs D.C (1977)	Pseudothecosomata	*Corolla spectabilis*	26	3	17	0.86	0.04	log y= a+b (logx); y=oxygen consumption [µl O2 h-1]; x=body protein [mg]; a & b = regression coefficients;	r2=coefficient of determination =0.97!! All measurements of respiration were standardized to protein rather than dry weight.
Biggs D.C (1977)	Pseudothecosomata	*Gleba cordata*	26	3	17	0.86	0.04		

			Weight [mg protein?]	µl O2 [mg protein-h-1]	SE	Oxygen consumption rate [g C g C-1 day-1]	
Biggs D.C (1977)	Pseudothecosomata	*Corolla spectabilis*	26	3	5	0.55	18.2
Biggs D.C (1977)	Pseudothecosomata	*Corolla spectabilis*	26	3	8	5.55	16.3
Biggs D.C (1977)	Pseudothecosomata	*Corolla spectabilis*	26	3	3	55.05	11
Biggs D.C (1977)	Pseudothecosomata	*Gleba cordata*	26	3	1	5.55	16.5
Biggs D.C (1977)	Pseudothecosomata	*Gleba cordata*	26	3	1	55.05	8.7

Reference	Order	Taxa	Temperature [°C]	n	Body weight [mg N ind-1]	SD	Oxygen consumption [µl O_2 ind-1 h-1]	SD	Oxygen consumption rate [g C g C-1 day-1]	Notes
Ikeda T. (1989)	Euthecosomata	*Limacina helicina*	0	2	0.052	0.027	0.451	0.216	0.023201244	AMRO2=metabolic rate adjusted to 1mg body nitrogen at the temperature 0 C; nitrogen chosen as the body mass unit since this reduces inter-specific variation in the relationship between metabolic rate and body mass. In order to calculate AMRO2 at = C, weight exponent of 0.85 and Q10 of 1.89 were assumed.
Ikeda T. (1989)	Euthecosomata	*Limacina antarctica*	-0.9	10	0.521	0.35	3.22	2.07	0.16564968	
Ikeda T. (1989)	Gymnosomata	*Clione limacina*	0	11	2.07	1.98	5.01	5.57	0.25773444	
Ikeda T. (1989)	Gymnosomata	*Clione antarctica*	-1.3	6	1.98	0.58	6.31	2.49	0.32461164	

It continues.

Continuing.

Reference	Order	Taxa	Temperature [°C]	SD	Regression equation	Dry body weight [mg] (excluding shell)	Total Oxygen consumption [µl O2 ind-1 day-1]	Oxygen consumption rate [g C g C-1 day-1]	Notes
Gilmer W.R. (1974)	Pseudothecosomata	*Gleba cordata*	26	0.5	log Y= 1.8-0.01 log X	80	1230	2.636505	Relationship between oxygen uptake in µl O_2/mg dry wt/h (X) dry wt (Y) of the animal plotted on a log-log scale.
Gilmer W.R. (1974)	Pseudothecosomata	*Gleba cordata*	20		log Y= 1.8-0.01 log X				
Gilmer W.R. (1974)	Thecosomata	*Cavolinia longirostris*	26	0.5	log Y=11.1-8.6 log X	0.45	60	0.12861	
Gilmer W.R. (1974)	Thecosomata	*Cavolinia longirostris*	20		log Y=11.1-8.6 log X				

B2) Growth rate as a function of temperature

Reference	Taxa	Temperature [°C]	Specific daily growth rate (G)	g= exponential growth coefficient	Growth rate [mm day-1]	DW [mg]	Growth rate [g C day-1]	Notes
Clarke C. and Roff J.C. (1990)	*Creseis virgula*		G= (eg-1)	0.015	0.015113065	0.000252546	6.31365E-08	"Growth rates were not directly estimated.There appeared to be only one estimate of growth rate for pteropod Creseis (C. virgula from Wells 1976), expressed as increase in shell length per day. Based on their length-weight relationship for C. virgula, they calculated g, but regarded it improbably low." (Clarke C. Roff J.C., 1990).

Reference	Taxa	Temperature [°C]	Lat/Long	Growth rate [mm month-1]	Growth rate [mm day-1]	DW [mg]	Growth rate [g C day-1]	Notes
Wells F.E. (1976)	*Creseis virgula conica*	27.029	13° 11' N/ 59° 41' W	0.3	0.01	0.000135873	3.39682E-08	Collections twice monthly, from june 1971-May 1973. from 300m to the surface (3 oblique tows)Every month max shell diameter of 300 L. inflata and max shell length of 200 C. virgula c. were measured, also max shell lenght of available individual L. bulimoides and L. trochiformis. The size-frequency data was plotted on probability paper-the method utilizes fluctuations in the numbers of individuals in the various size classes to determine growth rates (over short period of time).
Wells F.E. (1976)	*Limacina bulmoides*	27.029	13° 11' N/ 59° 41' W	0.15	0.005	4.8005E-05	1.20013E-08	
Wells F.E. (1976)	*Limacina inflata*	27.029	13° 11' N/ 59° 41' W	0.12	0.004	3.43419E-05	8.58548E-09	
Wells F.E. (1976)	*Limacina trochiformis*	27.029	13° 11' N/ 59° 41' W	0.1	0.003333333	2.612E-05	6.53001E-09	

It continues.

Continuing.

Reference	Taxa	Temperature [°C]	Growth [mm day-1], (L=shell diameter [mm], t=time (days))	Growth rate [mm day-1]	Dry weight [mg]	Growth rate [g C day-1]	Notes
Bednaršek N. et al. (2012a)	*Limacina helicina antarctica*	4	Growth= (Lt2-Lt1)/(t2-t1)	0.009	0.000115998	2.89995E-08	interseasonal
Bednaršek N. et al. (2012a)	*Limacina helicina antarctica*	4		0.006	6.31157E-05	1.57789E-08	interannual
Bednaršek N. et al. (2012a)	*Limacina helicina antarctica*	4		0.01	0.000135873	3.39682E-08	interannual
Bednaršek N. et al. (2012a)	*Limacina helicina antarctica*	4		0.009	0.000115998	2.89995E-08	interannual

Reference	Taxa	Temperature [°C]	Growth rate as the rate of 45Ca deposition in the shell [µg Ca deposited/mg Ca shell h-1]	Equation	Growth rate [g Ca gCa-1 shell day-1]	Notes
Fabry V.J. (1989)	*Clio pyramidata*	10.7 (* temperature was taken from the World Ocean Atlas database, as mean annual surface (0m) temperature at the given Lat/Long.)	1.1	Y=1.1 X; r2=0.73; X=time (h), Y=µg Ca deposition/mg Ca shell)	0.0264	G measured in the 45Ca uptake experiment.
Fabry V.J. (1989)	*Limacina helicina*	10.7 (* temperature was taken from the World Ocean Atlas database, as mean annual surface (0m) temperature at the given Lat/Long.	0.7		0.0168	G was calculated using data og Kobayashi (1974) on the mean shell diameter/month and the regression of the shell weight on shell diameter. (this estimate of growth rate is conservative - see pg.6)

B3) Ingestion rate as a function of temperature

Reference	Taxa	Temperature (at 200m) [°C]	Daily ingestion rate [I, ng (pigm.) ind-1 day-1]	Daily ingestion rate [I, g C day-1 gC-1]	Equation	Notes
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	>8.5 & <2.5 (PFZ)	7578.1	1.667182	I=kG/(1-b1); k=0.4047; 1/k=2.47; R sq=0.2532	k=gut evacuation rate [h-1]; R squared=coefficient of variance, 1/k=gut passage time (hour), b1=pigment destruction rate [nondimensional], G=integrated gut pigment concentration [ng (pigm) ind-1 day-1]; ind. (as weight in mg).

Reference	Taxa	Temperature (at 200m) [°C]	Daily ingestion rate [I, mg (pigm.) m-2 day-1]	Daily ingestion rate (I, g C day-1 gC-1)	Abundance [ind. m-2]	Gut evacuation rate [k, h-1]	Notes
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	8.5	1.513	1.666967147	199.68	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	8.5	2.018	1.667518029	266.24	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	8.5	0	0	0	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	8.5	0.595	1.667091187	78.52	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	8.5	2.503	1.667453973	330.24	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	8.5	0.815	1.667596726	107.52	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	8.5	0.064	1.666272189	8.45	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	8.5	0.453	1.668508287	59.73	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	8.5	1.94	1.6671875	256	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	8.5	0.272	1.669642857	35.84	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	2.5	0.048	1.65	6.4	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	2.5	0.175	1.671006944	23.04	0.405	Where temperature is given as 8.5 it is actually given as >8.5 in the article. Where the temperature is given as 2.5 it is actually given as <2.5 in the article. Temperature = subsurface (200 m).
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	2.5	0.097	1.6671875	12.8	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	2.5	0.33	1.668198529	43.52	0.405	
Bernard K.S. and Froneman P.W. (2005)	*Limacina retroversa*	2.5	0.694	1.667722556	91.55	0.405	

It continues.

Continuing.

Reference	Taxa	Temperature [°C]	Daily ingestion rate [ng pigm.	Daily ingestion rate [I, g C day-1 gC-1]	k [h-1]	Notes	
Pakhomov,E.A. and Perissinotto,R. (1997)	*Limacina spp.*	11.5	540.5	0.11891	0.355	The actual temperature given in the article was 11-12 °C.	
Pakhomov,E.A. and Perissinotto,R. (1997)	*Limacina spp.*	11.5	701.6	0.154352	0.355		
Pakhomov,E.A. and Perissinotto,R. (1997)	*Limacina spp.*	11.5	170	0.0374	0.355		
Reference	**Taxa**	**Temperature [°C]**	**Average dry mass [mg ind-1]**	**Daily ingestion rate [ng pigm. d-1]**	**k [h-1]**	**Daily ingestion rate [I, g C day-1 gC-1]**	**Notes**
Hunt B.P.V. et al. (2008)	*Limacina spp.*	9.5	0.2084	76.12	0.98	0.0167464	Original data from Perissinotto R. (1992), transformed in Hunt B.P.V. et al., 2008.
Hunt B.P.V. et al. (2008)	*Limacina spp.*	9.5	0.2084	301.87	0.98	0.0664114	
Hunt B.P.V. et al. (2008)	*Limacina spp.*	9.5	0.2084	31.22	0.98	0.0068684	
Hunt B.P.V. et al. (2008)	*Limacina spp.*	9.5	0.2084	134.01	0.98	0.0294822	

Reference	Taxa	Temperature [°C]	Lat/Long	Individual daily ingestion rate [ng (pigm.) ind-1 day-1]	Ingestion rate [g C gC-1 day-1]	Average daily individual DW [mg DW ind-1]	k [h-1]	Notes
Pakhomov E.A. and Froneman P.W. (2004)	*Clio sulcata*	-0.901	60° S/6 ° E	27757	6.10654	2.2	0.25	Daily ingestion rates (I, ng (pigm) ind. -1 d -1) were estimated from the relation: I = kG/(1-b'); where G is an integrated value (over a 24 h) of gut pigment content (ng (pigm) ind. -1), k= gut evacuation rate constant (h -1), b' = nondimensional index of the loss of pigment during digestion. Sampling conducted during December/January. Average k value of 0.25 h -1 for pteropods, determined during January 1995 in the Lazarev Sea (E.A. Pakhomov, unpublished), used for ingestion rate calculations.
Pakhomov E.A. and Froneman P.W. (2004)	*Limacina*	-0.901	60° S/6° E	2103	0.46266	2.2	0.25	
Pakhomov E.A. and Froneman P.W. (2004)	*Clio sulcata*	-0.544	56° 30' S/6° E	16627	3.65794	2.2	0.25	
		*temperature was taken from World Ocean Atlas Database (2005), as December mean surface (0 m) temperature at Lat/Long where sapling was conducted.						

It continues.

Continuing.

Reference	Taxa	Average temperature [°C]	Average daily ingestion rate [I, ng (pigm.) ind-1 day-1]	SD	Average Daily ingestion rate [I, g C gC-1 day-1]	Regression equation	Gut evacuation rate [k, h-1]	Notes
Bernard K.S. (2006)	*Limacina retroversa*	4.94	4146.51	1296.82	0.9122322	/	1.33	Daily ingestion rates of selected zooplankton [I, ng (pigm) ind-1 day-1] were estimated using the following equation (Perissinotto 1992): I = kG/(1-b1); I=ingestion rate, b1= gut pigment destruction rate [ng (pigm) ind-1)], k=gut evacuation rate [h-1]. The temperature was calculated as an average of sampling temperatures from each (one of the three) expeditions. Regression equations obtained from ingestion rates and integrated chl-a values measured during MOEVS II and IV expeditions were used to estimate ingestion rates of the copepods and pteropod for MOEVS V. ind. as weight in mg.
Bernard K.S. (2006)	*Limacina retroversa*	5.79	4128.68	892.23	0.9083096	/	1.33	
Bernard K.S. (2006)	*Limacina retroversa*	4.28	4196.88	8.56	0.9233136	y = 4 231.9551 – 4.4327 * x (p > 0.05); y = individual daily ingestion rate, x = integrated chl-a concentration	1.33	

B4) Mortality rate as a function of temperature

Reference	Taxa	Temperature [°C]	Annual Beta Mortality rate [year-1]	SD	Daily Beta mortality rate [day-1]	SD
Bednaršek N. et al. (2012a)	*Limacina helicina antarctica*	4	3.38	0.15	0.01	0

B5) TIC/TOC ration

Reference	Taxa	TIC/ TOC	TIC/TOC	SD	CaCO3:TOC (conversion factor of 8.33 for converting TIC to CaCO3)	TIC [mol]	TOC [mol]	TIC/TOC [mol/mol]	TIC/TOC [mol/mol]		
Bednaršek N. (2010)	*Limacina helicina antarctica*	0.27 : 0.73	0.369863014	0.0303	3.1 / 1	0.0225	0.060833	0.369863014	0.0225 : 0.0608		

Reference	Taxa	Stage	Mean Wet mass [mg ind.-1]	SD	n	Mean Dry mass [mg ind.-1]	SD	n	Mean Ash mass [mg ind.-1]	SD	n	PIC/POC*	PIC* [mol]	POC* [mol]	PIC/POC [mol/mol]	Notes
Gannefors C. et al. (2005)	*Limacina helicina*	juvenile	30.9	30.7	29	1.8	1.2	31	0.3	0	9	0.2	0.000025	0.000125	0.03 : 0.1	*PIC and POC were calculated** from the data in Gannefors C. et al. (2005).
Gannefors C. et al. (2005)	*Limacina helicina*	female	259.5	97.8	60	28.2	8.2	47	10.2	2.7	20	0.566667	0.00085	0.0015	0.9 : 1.5	
Gannefors C. et al. (2005)	*Limacina helicina*	female	293.7	77.3	40	33	8.9	50	/			/	/	/	/	
Gannefors C. et al. (2005)	*Limacina helicina*	female	332.5	149.8	71	33.9	12.8	48	14.9	5.1	29	0.784211	0.001242	0.001583	1.2 : 1.6	
Gannefors C. et al. (2005)	*Limacina helicina*	female	173.3	69.5	32	19.9	5.6	33	/			/	/	/	/	
Gannefors C. et al. (2005)	*Limacina helicina*	female	202.6	62.5	52	19.3	3.7	49	7.9	1.3	18	0.692982	0.000658	0.00095	0.7 : 0.95	

****Dry weight=all organics and inorganics; ash=inorganics, primarily CaCO3 (PIC - estimated from ash weight, assuming ash weight=CaCO3); Ash-free dry weight=all organics (Tsurumi M.et al., 2005)**

B6) Growth and Ingestion rate as a function of food concentration

Reference	Taxon	Temperature [°C]	Phytoplankton production [mg C m-3 h-1]	Food concentration [surface level) mg chla a m-3]	Daily ingestion rate [µg pigm. m-3 d-1]	Daily ing. rate/Food konc. [gC gC-1 day-1]	Gut evacuation rate [k=h-1]	Equation	Ingestion equation	Notes
Perissinotto R. (1992)	*Limacina sp.*	9.5	1.2	2	23.6	0.649	0.98	Chl a ingestion = (ing. rate/food konc.)* 55 g Chl	I=KG/(1-b');K=gut evacuation rate(day-1), G=pigment measureable in the gut;b'=non dimensional index for loss of pigment in digestion.	No measurements of K were carried out for year 1985 (first two I values) - cause of error. Pg. 11! The community grazing impact for 1985 was then obtained by multiplying the gut pigment levels of C measured in 1989 by an average factor of 8.9 for the Natal Bank and 11.7 for the offshore samples. Temperature was taken from the experiments for obtaining K (=gut evacuation rate)!
Perissinotto R. (1992)	*Limacina sp.*	9.5	0.7	1	32.3	1.7765	0.98			
Perissinotto R. (1992)	*Limacina sp.*	9.5	<0.4	0.2	6.9	1.8975	0.98			
Perissinotto R. (1992)	*Limacina sp.*	9.5	<0.4	0.3	18.5	3.391667	0.98			

Reference	Taxon	Temperature [°C]	Phytoplankton production [mg C m-2 day-1g	Phytoplankton biomass [mg Chla a m-2]	Daily ingestion rate [ng pigm. ind.-1 d-1]	Daily ingestion rate [gC g C-1 d-1]	k [h-1] (gut evacuation rate)	Equation	Notes
Pakhomov E.A. and Perissinotto R. (1997)	*Limacina spp.*	11.5	278.2	34.3	540.5	0.000867	0.355	I=k G/(1-b'); G=integrated value (over 24h period) of gut pigment contents (ng (pigm) ind.-1), b'=nondiemnsional index of the loss of pigemnt during digestion	
Pakhomov E.A. and Perissinotto R. (1997)	*Limacina spp.*	11.5	261.4	45.9	701.6	0.000841	0.355		
Pakhomov E.A. and Perissinotto R. (1997)	*Limacina spp.*	11.5	274.3	32.3	170	0.000289	0.355		Temperature was between 11-12!

B7) Threshold food concentration and food preference

Reference	Order	Taxa	Food maintainance requirements [mg food ind. -1 day-1]	Amounnt of food expressed as % of dry body weight per ind.	Notes
Gilmer,W.R. (1974)	Pseudothecosomata	*Gleba cordata*	0.6-1.5	0.7-1.8 %	In both cases, the lower value of food maintenance requirements given is that for a strictly fat diet and the higher value given is for pure carbohydrate uptake.
Gilmer,W.R. (1974)	Pseudothecosomata	*Gleba cordata*			
Gilmer,W.R. (1974)	Thecosomata	*Cavolinia longirostris*	0.03-0.07	6.6-15.5 %	
Gilmer,W.R. (1974)	Thecosomata	*Cavolinia longirostris*			

Reference	Order	Taxa	Food source	Additional info
Gilmer R.W. and Harbison G.R. (1991)	Thecosomata	*Limacina helicina*	suspended material, motile prey (tintinnids, copepods, juvenile Limacina helicina)	It is possible the smaller specimen are herbivores and switch to omnivory at larger sizes. At large sizes L. helicina is opportunistic feeder. Crustacean prey might increase with the size of L. helicina.
Gilmer R.W. and Harbison G.R. (1991)	Thecosomata	*Juvenile Limacina helicina*	small suspended particles (phytoplankton and protozoans) and possibly also on suspended detritus.	
Gannefors C. et al. (2005)	Thecosomata	*Veliger Limacina helicina*	particulate organic matter	POM is an important dietary component in this stage of life cycle.
Flores H. et al. (2011)	Thecosomata	*Limacina helicina*		Limacina helicina mainly feed on phytoplankton in summer,but little is known how they survive the winter in Antarctic ice-covered waters (Lalli and Gilmer, 1989). In the Arctic, juvenile L. helicina have been reported to rely on particulate organic matter originating from the sea ice in winter (Gannefors etal.,2005;Kobayashi,1974). If that is alsothe case in the Southern Ocean, L. helicina is likely to concentrate under ice in winter and prefer the phytoplankton-rich open waters in summer.

It continues.

Continuing.

Reference	Order	Taxa	Food source	Additional info	Notes
Hunt B.P.V. et al. (2008)	Thecosomata	*Limacina retroversa*	Diatoms, Dinoflagellates, Coccolithophorid, Tintinnids	Dominance of diatoms, dinoflagellates and microzooplankton.	Data taken from the Hunt B.P.V. et al. (2008), Table 4. where the data source was Boas (1886, in Lalli and Gilmer, 1989);
Hunt B.P.V. et al. (2008)	Thecosomata	*Clio pyramidata f. sulcata*	Diatoms, Dinoflagellates, Tintinnids, Foraminiferans, Copepods, Polychaetes, Sillicoflagellates	Diatoms important part of diet - prodominatly herbivorous diet, but also larger motile organism contribute a substantial part of food - larger specimen of could have more omnivorous diet.	Data taken from the Hunt B.P.V. et al. (2008), Table 4. where the data source was Hopkins and Torres (1989);
Hunt B.P.V. et al. (2008)	Gymnosomata	*Clione limacina antarctica*	Limacina helicina		Data taken from the Hunt B.P.V. et al. (2008), Table 4. where the data source was Hopkins (1987);
Hunt B.P.V. et al. (2008)	Thecosomata	*Limacina helicina antarctica*	Diatoms, Dinoflagellates	Diet phytoplankton dominated, but theres also some carnivory noted.	Data taken from the Hunt B.P.V. et al. (2008), Table 4. where the data source was Hopkins (1987), Hart (in Morton, 1954);
Hunt B.P.V. et al. (2008)	Gymnosomata	*Clione limacina antarctica*	Limacina helicina antarctica	In the northern hemisphere C. limacina feeds on L. helicina in polar waters and L. retroversa in sub-polar/temperate waters (Lalli and Gilmer, 1989), and it is probable that C. limacina antarctica also feeds on L. retroversa australis in the SAZ and PFZ waters of the Southern Ocean.	Data taken from the Hunt et al. Article, Table 4. where the data source was Hopkins (1987);
Hunt B.P.V. et al. (2008)	Gymnosomata	*Clione limacina veligers*	phytoplankton	In the northern hemisphere, veliger stages of C. limacina were the only stage not feeding on Limacina. After metamorphosis from veliger to polytochous larvae (at 0.3 mm lenght), they begin feedin on Limacina veliger.	Data source Lalli and Gilmer(1989).
Hunt B.P.V. et al. (2008)	Gymnosomata	*S. australis*	specialist predator on C. pyramidata	No gut content data available.	Data source Lalli and Gilmer (1989).

It continues.

Continuing.

Reference	Order	Taxa	Food source	Additional info
Böer M. et al. (2005)	Gymnosomata	*Clione limacina*	Limacina helicina exclusively (monophagy!)	Due to monophagy C. limacina is exposed to long periods of food scarcity and consequently has to be adapted to starvation stress. Starvation experiments with C. limacina revealed that this species is able to survive in an aquarium for nearly a year without food. C. limacina has evolved various strategies as body shrinkage, utilisation of body constituents not essential for survival, a very low metabolism and slow lipid consumption.
Marine species indentification portal (http://species-identification.org)	Pseudothecosomata	*Corolla spectabilis*	A preference for particles > 10µm seems to occur.	
Marine species indentification portal (http://species-identification.org)	Gymnosomata	*Pneumodermopsis spp.*	This carnivorous species of Pneumodermopsis paucidens p. feeds on Limacina bulimoides and especially Creseis spp.	Pneumodermopsis is a genus with fourteen species which are difficult to identify.
Marine species indentification portal (http://species-identification.org)	Thecosomata	*Diacria trispinosa*	small plankton mainly phytoplankton in the epi- and mesopelagic zone	
Marine species indentification portal (http://species-identification.org)	Thecosomata	*Cuvierina columnella atl.*	Copepod naupli, tintiniids, thecate dinoflagellates, Globigerina and centric diatoms were found in the gut.	
Marine species indentification portal (http://species-identification.org)	Thecosomata	*Limacina helicoides*	The following organisms were found as food: Fragilariopsis antarctica, Thalassiosira, fragments of Coscinodiscus and Chaetoceros.	The recordings of food organisms indicate that planktonic organisms up to about 40 µm are caught as food, while other large organisms seem to be rejected as they were found in the surrounding plankton but not in the alimentary system i.e. larger specimens of Chaetoceros with bristles 1000µm long, and large dinoflagellates.
Marine species indentification portal (http://species-identification.org)	Gymnosomata	*Thliptodon gegenbauri*	Carnivore	

ANNEX C

C1) Studies of carbonate/aragonite budgets and production

Producer	Global C biomass at any point of time	Global C (biomass) production estimate [Pg C yr-1]	CaCO3 carbon/Inorganic carbon production (specified in the unit)	Net aragonite (CaCO3) production	Area	Reference	Origin od data/Technique
Pteropods	444 Tg C	444 Tg C yr-1	998.6 Tg CaCO3 yr-1	828.838 Tg CaCO3 yr-1	322x10e+6 km2 (min area), global	Bednaršek N. et al., 2012c	net tows (abundance/biomass data)
Pteropods	505 Tg C	505 Tg C yr-1	1135.8 Tg CaCO3 yr-1	942.714 Tg CaCO3 yr-1	362.03x10e+6 km2 (max area), global	Bednaršek N. et al., 2012c	net tows (abundance/biomass data)
Coccolithophores	3.8 +-21.0 µg C L-1 (mean)				global	O'Brien C.J. et al., 2012	abundance measurements
Coccolithophores	0.25 µg C L-1 (median)				global	O'Brien C.J. et al., 2012	abundance measurements
Coccolithophores			7.3-14.6 g CaCO3 m-2 yr-1		subarctic Pacific	Fabry V.J., 1989	instantaneous growth rate, model
Global (total)			12-20 g g CaCO3m-2 yr-1		subarctic Pacific	Fabry V.J., 1989	instantaneous growth rate, model
Pteropods (aragonite)				0.091 - 0.30 g m-2 yr-1 (0.25 mg - 0.83 mg C m-2 d-1)	Pacific (Central - Equatorial)	Fabry V. 1989, 1990 (from Gangstø R. et al., 2008)	net samples (abundance/biomass)
Foraminifers	0.85-3.27 Tg C	25-100 Tg C yr-1 (8.5-32.7 Tg C yr-1 without 12-125 µm organisms)		Foraminifers	290x10e+6 km2	Schiebel R. and Movellan A., 2012	net samples (abundance/biomass)
Foraminifers	0.94-3.63 Tg C			Foraminifers	322x10e+6 km2 (marginal basins included)	Schiebel R. and Movellan A., 2012	net samples (abundance/biomass)
Coccolithophores			1.1+-0.3 Pg PIC yr-1	Coccolithophores	global	Feely R.A. et al., 2004	Seasonal cycle of euphotic zone alkalinity
Global			0.8-1.4 Pg CaCO3-C (PIC) yr-1	Global	global	Feely R.A. et al., 2004	Seasonal cycle of euphotic zone alkalinity

It continues.

Continuing.

Producer	Global C biomass at any point of time	Global C (biomass) production estimate [Pg C yr-1]	CaCO3 carbon/Inorganic carbon production (specified in the unit)	Net aragonite (CaCO3) production	Area	Reference	Origin od data/Technique
Foraminifers			0.36-0.065 Pg C yr-1	Foraminifers	290 x10e+12 m2	Schiebel R., 2002	multinet and sediment trap flux data at 500 m (no production rate data)
Fish (pelagic)			0.04-0.11 Pg C yr-1	Fish (pelagic)	300 10e+12 m2	Wilson R.W. et al., 2009	model output
Molluscs (neritic)			0.047 Pg C yr-1	Molluscs (neritic)	1.8 10e+12 m2	Chauvaud L. et al., 2003	global extrapolation based on data from three stations off California over a period of 7 years
Global			0.87 Pg C yr-1	Global	global	Gangstø R. et al., 2008	Model
Echinoderms (shelves)			0.093 Pg C yr-1 (0.78 Pg CaCO3 yr-1)	Echinoderms (shelves)	10x10e+12 m2	Lebrato M. et al., 2010	global extrapolation is based on data from 523 stations.
Echinoderms (slopes)			0.0078 Pg C yr-1 (0.065 Pg CaCO3 yr-1)	Echinoderms (slopes)	32x10e+12 m2	Lebrato M. et al., 2010	global extrapolation is based on data from 523 stations.
Echinoderms (abyssal)			0.0019 Pg C yr-1 (0.016 Pg CaCO3 yr-1)	Echinoderms (abyssal)	290x10e+12 m2	Lebrato M. et al., 2010	global extrapolation is based on data from 523 stations.
Echinoderms Total			0.102 Pg C yr-1 (0.0861 Pg CaCO3 yr-1)	Echinoderms Total	332x10e+12 m2	Lebrato M. et al., 2010	global extrapolation is based on data from 523 stations.
Global (excluding cocco.)			0.96-2.56 Pg C yr-1	Global (excluding cocco.)	global	Lebrato M. et al., 2010	global extrapolation is based on data from 523 stations.
Global net		6.7-9.1 and 8.0-10.8 Gt C yr-1	1.1 +-0.3 Gt C yr-1	Global net	global (coastal regions not included for CaCO3 estimate)	Lee K., 2001	community production from decrease in salinity (S)-normalized total DIC inventory, global extrapolation of multiyear sediment trap data

It continues.

Continuing.

Producer	Global C biomass at any point of time	Global C (biomass) production estimate [Pg C yr-1]	CaCO3 carbon/Inorganic carbon production (specified in the unit)	Net aragonite (CaCO3) production	Area	Reference	Origin od data/Technique
Coral Reefs (Neritic)			0.108 Pg C yr-1	Coral Reefs (Neritic)	0.6 x10e+12 m2	Iglesias-Rodrigues M.D. et al., 2002	origin of data in Milliman J.D. (1993)
Halimeda bioherms (Neritic)			0.02 Pg C yr-1	Halimeda bioherms (Neritic)		Iglesias-Rodrigues M.D. et al., 2002	origin of data in Milliman J.D. (1993)
Banks/bays (Neritic)			0.048 Pg C yr-1	Banks/bays (Neritic)	0.8 x10e+12 m2	Iglesias-Rodrigues M.D. et al., 2002	origin of data in Milliman J.D. (1993)
Non-carbonate shelves			0.05 Pg C yr-1	Non-carbonate shelves	1.5 x 10e+12 m2	Iglesias-Rodrigues M.D. et al., 2002	
Shelves			0.024 - 0.120 Pg C yr-1	Shelves	10 x 10e+12 m2	Iglesias-Rodrigues M.D. et al., 2002	origin of data in Milliman J.D. (1993)
Slopes			0.06 Pg C yr-1	Slopes	32 x 10e+12 m2	Iglesias-Rodrigues M.D. et al., 2002	origin of data in Milliman J.D. (1993)
Coccolithophores			1.6 +- 0.3 Pg PIC yr-1 (annual global calcification)		global	Balch W.M. et al., 2007	satellite-determined parameters, photosythesis rate determinants
Global			1.1 Pg PIC yr-1			Wollast R., 1994 (from Balch W.M. et al., 2007)	chemichal state of the cabon system
Global			1.0 Pg PIC yr-1			Morse J.W. and Mackenzie F.T., 1990 (from Balch W.M. et al., 2007)	geochemistry of sedimentary carbonates
Total Open Ocean			6.9-7.9 mg C m-2 d-1			Morse J.W. and Mackenzie F.T., 1990 (from Gangstø r. et al., 2008)	
Global			1.0 Pg PIC yr-1			Archer D. and Maier-Reimer E., 1994 and Archer 1996b (from Balch W.M. et al., 2007)	Gridded maps of calcite and diagenetic odel of CaCO3 perservation
Global			1.1 Pg PIC yr-1			Moore J.K. et al., 2002 (from Balch et al., 2007)	global marine ecosystem mixe-layer model
Global			0.6 Pg PIC yr-1			Milliman J.D., 1993 (from Balch W.M. et al., 2007)	historical accumulation rates and sediment trap data
Open Ocean			0.4-20 mg C m-2 d-1 (aragonite contribution excluded)			Milliman J.D., 1993 (from Gangstø R. et al., 2008)	
Global			0.7 Pg PIC yr-1			Milliman J.D. et al., 1999 (from Balch W.M. et al., 2007)	historial accumulation rates and sediment trap data

C2) Studies of carbonate/aragonite production, dissolution and export

Producer	Global C (biomass) production estimate [Pg C yr-1]	CaCO3 carbon/Inorganic carbon production (specified in the unit)	Net aragonite (CaCO3) production	CaCO3 export (flux)	Aragonite (CaCO3) export (flux)	Dissolution	Area	Reference	Origin od data/Technique
Global	0.85 Pg C yr-1		0.30 Pg C yr-1 (or 35% of total net CaCO3 production)	0.62 Pg C yr-1	0.21 Pg C yr-1	0.55 Pg C yr-1 (CaCO3 dissolution); 0.18 Pg C yr-1 (aragonite dissolution); 0.37 Pg C yr-1(calcite dissolution)	global	Gangstø R. et al., 2008	model
Global (pelagic)				0.6 Pg C yr-1 (0.6 Gt PIC yr-1)			< 100 m	Sarmiento J.L. et al., 2002	based on vertical alcalinity and nitrate gradients combined with Laws et al (2000) of POC export
Pelagic				0.4 +- 0.05 Pg C yr-1			< 2000 m	Honjo S. et al., 2008	sediment trap flux data
Pelagic				0.4-1.8 Pg C yr-1				Moore J.K. et al., 2004	export from models
Coccolithophores (pelagic)				0.6-1.6 +- 0.3 Pg C yr-1			300x10e+12 m2(euphotic zone)	Balch W.M. et al., 2007	satellite-determined parameters, photosythesis rate determinants, satellite production estimation
Foraminifers		3.5 g CaCO3 m-2 yr-1					subarctic Pacific	Fabry V.J., 1989	sediment trap data of Thunel and Honjo, 1987
Pteropods (aragonite)			0.8-1.6 g CaCO3 m-2 yr-1			35 to 62 mg CaCO3 m -2 d -1 (accoring to Tsunogai, 1978; Fiadeiro, 1980; Tsunogaiand Watanabe1981; Chen et al., 1986 from Fabry 1989)	subarctic Pacific	Fabry V.J., 1989	instantaneous growth rate, model

It continues.

Continuing.

Producer	Global C (biomass) production estimate [Pg C yr-1]	CaCO3 carbon/Inorganic carbon production (specified in the unit)	Net aragonite (CaCO3) production	CaCO3 export (flux)	Aragonite (CaCO3) export (flux)	Dissolution	Area	Reference
Global		0.5-1.6 Gt PIC yr-1		0.4-1.8 Gt PIC yr-1 (models); 1.4-4.7 Gt PIC yr-1 (traps, Pacific); 0.6+-0.4 Gt PIC yr-1 (export to traps below 2000 m)			global (euphotic zone CaCO3 production)	Berelson W.M., 2007
Global		4.3 Gt PIC yr-1						Balch W.M. and Kilpatrick K.A., 1996
Pteropods (Clio pyramidata, Limacina helicina)					2.5 g CaCO3 m-2 yr-1		regional (North Pacific)	Tsurumi M. et al., 2005
Pteropods (?)					0.83 - 1.8 g C m-2 yr-1 (2.3-4.9 mg C m-2 d-1)		North Pacific	Betzer P.R. et al., 1984 (from Gangstø R. et al.., 2008)
Dissolution in 200-1500 m						1 Pg IC yr-1	300x10xe+12 m2 (Atlantic, Pacific, Indian)	Berelson W.M., 2007
Dissolution in the Seafloor, >2000 m						0.4+-0.03 Pg IC yr-1	300x10xe+12 m2	Berelson W.M., 2007
Burial in Holocene sediments						0.1 Gt PIC yr-1		Berelson W.M., 2007
Total pelagic dissolution						0.5 +- 0.2 Pg CaCO3-C yr-1		Feely R.A. et al., 2004
Total dissolution						0.55 Pg C yr-1 (CaCO3 dissolution); 0.18 Pg C yr-1 (aragonite dissolution); 0.37 Pg C yr-1(calcite dissolution)		Gangstø R. et al., 2008
Dissolution 0-2000 m						0.34 Pg C yr-1 (CaCO3 dissolution); 0.15 Pg C yr-1 (aragonite dissolution); 0.18 Pg C yr-1 (calcite dissolution)		Gangstø R. et al., 2008

ANNEX D

Published paper

Bednaršek N., Možina J., Vogt M., O'Brien C., Tarling G.A. 2012. The global distribution of pteropods and their contribution to carbonate and carbon biomass in the modern ocean. *Earth System Science Data,* 4, 167-186

Earth Syst. Sci. Data, 4, 167–186, 2012
www.earth-syst-sci-data.net/4/167/2012/
doi:10.5194/essd-4-167-2012

Open Access Earth System Science Data

The global distribution of pteropods and their contribution to carbonate and carbon biomass in the modern ocean

N. Bednaršek[1], J. Možina[2], M. Vogt[3], C. O'Brien[3], and G. A. Tarling[4]

[1]NOAA Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115, USA
[2]University of Nova Gorica, Laboratory for Environmental Research, Vipavska 13, Rožna Dolina, 5000 Nova Gorica, Slovenia
[3]Institute for Biogeochemistry and Pollutant Dynamics, ETH Zürich, Universitaetstrasse 16, 8092 Zürich, Switzerland
[4]British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Correspondence to: N. Bednaršek (nina.bednarsek@noaa.gov)

Received: 20 March 2012 – Published in Earth Syst. Sci. Data Discuss.: 10 May 2012
Revised: 8 October 2012 – Accepted: 19 October 2012 – Published: 10 December 2012

Abstract. Pteropods are a group of holoplanktonic gastropods for which global biomass distribution patterns remain poorly described. The aim of this study was to collect and synthesise existing pteropod (Gymnosomata, Thecosomata and Pseudothecosomata) abundance and biomass data, in order to evaluate the global distribution of pteropod carbon biomass, with a particular emphasis on temporal and spatial patterns. We collected 25 939 data points from several online databases and 41 scientific articles. These data points corresponded to observations from 15 134 stations, where 93 % of observations were of shelled pteropods (Thecosomata) and 7 % of non-shelled pteropods (Gymnosomata). The biomass data has been gridded onto a $360 \times 180°$ grid, with a vertical resolution of 33 depth levels. Both the raw data file and the gridded data in NetCDF format can be downloaded from PANGAEA, doi:10.1594/PANGAEA.777387. Data were collected between 1950–2010, with sampling depths ranging from 0–2000 m. Pteropod biomass data was either extracted directly or derived through converting abundance to biomass with pteropod-specific length to carbon biomass conversion algorithms. In the Northern Hemisphere (NH), the data were distributed quite evenly throughout the year, whereas sampling in the Southern Hemisphere (SH) was biased towards winter and summer values. 86 % of all biomass values were located in the NH, most (37 %) within the latitudinal band of 30–60° N. The range of global biomass values spanned over four orders of magnitude, with mean and median (non-zero) biomass values of 4.6 mg C m^{-3} (SD = 62.5) and 0.015 mg C m^{-3}, respectively. The highest mean biomass was located in the SH within the 70–80° S latitudinal band (39.71 mg C m^{-3}, SD = 93.00), while the highest median biomass was in the NH, between 40–50° S (0.06 mg C m^{-3}, SD = 79.94). Shelled pteropods constituted a mean global carbonate biomass of 23.17 mg $CaCO_3$ m^{-3} (based on non-zero records). Total biomass values were lowest in the equatorial regions and equally high at both poles. Pteropods were found at least to depths of 1000 m, with the highest biomass values located in the surface layer (0–10 m) and gradually decreasing with depth, with values in excess of 100 mg C m^{-3} only found above 200 m depth.

Tropical species tended to concentrate at greater depths than temperate or high-latitude species. Global biomass levels in the NH were relatively invariant over the seasonal cycle, but more seasonally variable in the SH. The collected database provides a valuable tool for modellers for the study of marine ecosystem processes and global biogeochemical cycles. By extrapolating regional biomass to a global scale, we established global pteropod biomass to add up to 500 Tg C.

Published by Copernicus Publications.

1 Introduction

The phylum Mollusca comprises at least 100 000 species, of which only 4000 species inhabit the upper ocean, principally those in the class Gastropoda. Approximately 140 species are holoplanktonic, meaning that they do not inhabit the seabed during any stage of their life cycle. The holoplanktonic lifestyle is facilitated by adaptations such as the development of swimming appendages and the reduction or loss of the calcareous shell. The pteropods are holoplanktonic gastropods that are widespread and abundant in the global ocean (Lalli and Gilmer, 1989). They consist of two orders: the Thecosomata (shelled pteropods) and the Gymnosomata (naked pteropods). The two orders are taxonomically separated not only by their morphology and behaviour, but also by their trophic position within the marine food web, with the former consisting mainly of herbivores and detritivores (Hopkins, 1987; Harbison and Gilmer, 1992) and the latter of carnivores (Lalli, 1970). A further systematic detail divides order Thecosomata into two suborders, the Euthecosomes and Pseudothecosomes. The two suborders have similar lifestyles, but they are set apart by their anatomical characteristics, most notably a gelatinous internal pseudoconch in Pseudothecosomes that replaces the external shell present in Euthecosomes (Lalli and Gilmer, 1989).

Pteropods have high ingestion rates that are in the upper range for mesozooplankton (Perissinotto, 1992; Pakhomov and Perissinotto, 1997). Although pteropods constitute, on average, only 6.5 % of the total abundance density of grazers in areas such as the Southern Ocean, they contribute on average 25 % to total phytoplankton grazing and consume up to 19 % of daily primary production (Hunt et al., 2008). Pteropods themselves are also an important prey item for many predators, such as larger zooplankton as well as herring, salmon and birds (Hunt et al., 2008; Karnovsky et al., 2008).

Pteropods are also involved in numerous pathways of organic carbon export. They contribute to the downward flux of carbon through the production of negatively buoyant faecal pellets. A number of pteropods also produce pseudo-faeces, i.e. accumulations of rejected particles expelled in mucous strings (Gilmer, 1990). Pteropods feed using mucous webs that trap fine particles and small faecal pellets, which form fast sinking colloids when abandoned (Jackson et al., 1993; Gilmer and Harbison, 1991). Pteropods actively transport carbon downwards during the descent phase of nycthemeral migrations, mostly from the shallow euphotic zone into the deeper twilight zone, where they respire and defecate.

In terms of inorganic carbon, pteropods are one of only a few taxa that make their shells out of aragonite as opposed to the calcite form of calcium carbonate. The biogeochemical importance of aragonite production by pteropods has been shown in a number of studies (Berner and Honjo, 1981; Acker and Byrne, 1989). Their aragonite shell not only contributes to the transfer of inorganic material into the deep ocean (Tréguer et al., 2003) but also increases the weight of pteropods as settling particles and hence their sinking speed (Lochte and Pfannkuche, 2003). Ontogenetic (or seasonal) migration, often followed by mass mortality, transports both organic and inorganic carbon to depth (Tréguer et al., 2003). On a global scale, aragonite production by pteropods might constitute at least 12 % of the total carbonate flux worldwide (Berner and Honjo, 1981).

Although the ecological and biogeochemical importance of pteropods has been well recognised, essential details on their global biomass distribution remain poorly resolved. Such information is required for modellers to be able to incorporate this group as a plankton functional type within ecosystem models and to allow the quantification of their contribution to carbon export in biogeochemical models.

The Marine Ecosystem Model Inter-comparison Project (MAREMIP) has been launched as an initiative to compare current plankton functional type models, and to collect data necessary for their validation. In 2009, MAREMIP launched the MARine Ecosystem DATa project, with the aim to construct a database based on field measurements for the biomass of ten major plankton functional types (PTFs) currently represented in marine ecosystem models (Le Quéré et al., 2005). The resulting biomass databases include diatoms (silicifiers), *Phaeocystis* (DMS producers), coccolithophores (calcifying phytoplankton), diazotrophs (nitrogen fixers), picophytoplankton, bacterioplankton, mesozooplankton, macrozooplankton and pteropods and foraminifera (calcifying zooplankton). All MAREDAT data sets of global biomass distribution are publicly available and will serve marine ecosystem modellers for model evaluation, development and future model inter-comparison studies. This study will present and evaluate the seasonal and temporal distribution of pteropod carbon biomass, with a particular emphasis on the seasonal and vertical biomass patterns. Finally, global estimates of pteropod biomass and productivity will be presented.

2 Data

2.1 Origin of data

The sources of the data were several online databases (PANGEA, ZooDB, NMFS127 COPEPOD) and 41 scientific articles. The full data set is comprised of 25 939 data points (Table 1). Each data point includes the following information: Year, Month, Day, Longitude, Latitude, Sampling Depth (m), Mesh size (μm) Abundance (ind. m^{-3}) and Biomass (mg C m^{-3}) and the data source. All data points presenting abundance measurements were later converted to biomass values. Zero biomass values were included as biologically valid data points in the data set. Some data sets included multiple samples at several stations, which would bias the global biomass estimates if not suitably treated. Thus, when repeat sampling of the same station location

Table 1. The list of data contributors in alphabetical order, with the two major online databases listed at the end of the list.

Entry No.	Principal Investigator	Database	Year (data collection)	Region
1	Andersen et al. (1997)	PANGEA	1991–1992	NE tropical Atlantic
2	Bednaršek et al. (2012)	–	1996–2010	Southern Ocean (Scotia Sea)
3	Bernard and Froneman (2005)	–	2004	Southern Ocean (west-Indian sector of the Polar Frontal Zone)
4	Bernard and Froneman (2009)		2002/2004/2005	Indian sector PFZ
5	Blachowiak-Samolyk et al. (2008)	–	2003	Arctic (N Svalbard waters)
6	Boysen-Ennen et al. (1991)	–	1983	Antarctica (Weddell Sea)
7	Broughton and Lough (2006)	–	1997	North Atlantic (Georges Bank)
8	Clarke and Roff (1990)	–	1986	Caribbean Sea (Lime Cay)
9	Daase and Eiane (2007)	–	2002–2004	Arctic (N Svalbard waters)
10	Dvoretsky and Dvoretsky (2009)	–	2006	E Barents Sea (Novaya Zemlya)
11	Elliot et al. (2009)	–	2006–2007	Antarctica (McMurdo Sound)
12	Flores et al. (2011)	–	2004–2008	Southern Ocean (Lazarev Sea)
13	Foster (1987)	–	1985	Antarctica (McMurdo Sound)
14	Froneman et al. (2000)	–	1998	Southern Ocean (Prince Edward Archipelago)
15	Hunt and Hosie (2006)	–	2001–2002	Southern Ocean (south of Australia)
16	Koppelmann et al. (2004)	PANGEA	1999	Eastern Mediterranean Sea
17	Marrari et al. (2011)	–	2001/2002	W Antarctic (Marguerite Bay)
18	Mazzocchi et al. (1997)	PANGEA	1991–2002	Eastern Mediterranean Sea
19	Mileikovsky (1970)	–	1966	North Atlantic, Subarctic and North Pacific Ocean
20	Moraitou-Apostolopoulou et al. (2008)	PANGEA	1994	Eastern Mediterranean Sea
21	Mousseau et al. (1998)	–	1991–1992	NW Atlantic (Scotian Shelf)
22	Nishikawa et al. (2007)	–	2000–2002	Pacific Ocean (Sulu Sea, Celebes Sea, South China Sea)
23	Pakhomov and Perissinotto (1997)	–	1993	Southern Ocean (Subtropical Convergence)
24	Pane et al. (2004)	–	1995	Antarctica (Ross Sea)
25	Fernandez de Puelles et al. (2007)	–	1994–2003	Western Mediterranean
26	Ramfos et al. (2008)	PANGEA	2000	Eastern Mediterranean
27	Rogachev et al. (2008)	–	2004	W Pacific Ocean (Academy Bay, Sea of Okhotsk)
28	Schalk (1990)	–	1984–1999	Indo-Pacific waters (E Banda Sea, W Arafura Sea)
29	Schiebel et al. (2002)		1997/1999	S of Azores Islands
30	Schnack-Schiel and Cornils (2009)	PANGEA	2005	Pacific Ocean (Java Sea)
31	Siokou-Frangou et al. (2008)	PANGEA	1987–1997	Eastern Mediterranean
32	Solis and von Westernhagen (1978)	–	1972	Philippines (Hilutangan Channel)
33	Swadling et al. (2011)	–	2004–2008	E Antarctica (Dumont d'Urville Sea)
34	Volkov (2008)	–	1984–2006	Okhotsk Sea, Bering Sea, NWP
35	Ward et al. (2007)	–	2004–2005	Southern Ocean (S&W of Georgia)
36	Wells Jr. (1973)	–	1972	N Atlantic Ocean (Barbados)
37	Werner (2005)	–	2003	Arctic (W Barents Sea)
38	Wormuth (1985)	–	1975–1977	N Atlantic Ocean (NW Sargasso Sea)
39	Zervoudaki et al. (2008)	PANGEA	1997–2000	Eastern Mediterranean
40	NMFS-COPEPOD (2011) NOAA (National Oceanic and Atmospheric Administration)	COPEPOD – The global plankton database	1953–2001	Global data set
41	ZooDB (2011), Ohman	ZooDB – Zooplankton database	1951–1999	Pacific Ocean (Southern and Central California)

was conducted in a single day (for instance through sampling both night and day or with different mesh-sized nets), a mean biomass at that station was calculated and used in subsequent processing. As the sampling methodology can introduce major errors in the biomass estimates, a systematic characterisation of the sampling gear, was also included to allow sources of error to be identified. In addition, all details on pteropod species composition and life stages were

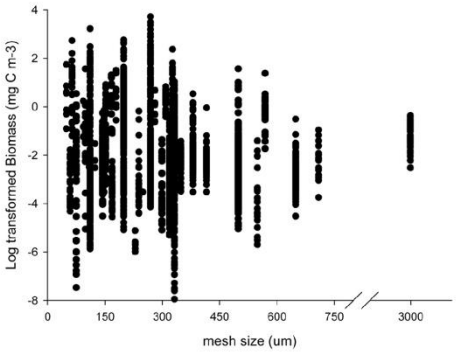

Figure 1. The relationship between net mesh size and pteropod biomass.

documented within the database. Where there were a number of species identified per station, we also provided summary statistics of total pteropod biomass per station (n = 14 136). The database included both Gymnosomata and Thecosomata, encompassing all genera included in the taxonomic tree, which was taken from Marine Species Identification Portal (http://species-identification.org) presented in Fig. 3. Further subspecies levels (or formae) were not resolved within the database. No observations of the suborder Pseudothecosomata were reported in the source data sets.

2.2 Quality control

The identification and rejection of statistical outliers in the summarised biomass data set was performed using Chauvenet's criterion (Glover et al., 2011; Buitenhuis et al., 2012). Based on this statistical analysis, none of the stations were excluded as outliers (two sided z-score = 4.1257).

2.3 Methodology for biomass conversion

Of the data sets obtained, the majority only reported values for abundance (ind. m^{-3}), with very few providing biomass values (mg m^{-3}). Furthermore, abundance data was collected with varying mesh sizes and net-sampling strategies, which might introduce uncertainties. Therefore, we have reported the mesh sizes and net sampling strategy in the database whenever this information was available (PANGEA Table). In certain cases, multiple mesh-sized samplers were used, of which we have included all descriptions available. No data were excluded on the basis of mesh size and we examine the influence of mesh size in the Results section (Figs. 1 and 2).

Where direct biomass values were not available, we calculated biomass as a product of abundance and dry weight (DW, mg). To estimate DW, the length (L, mm) of organisms

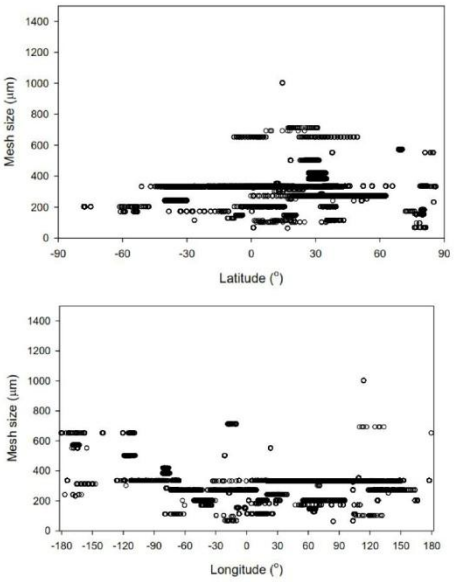

Figure 2. Net-mesh size versus longitude (above) and latitude (below). Data was excluded if multiple mesh sizes were reported.

was first converted to wet weight (WW, mg) using various conversions (see below), with subsequent conversion to dry weight (Table 2).

For many pteropod species, specific length-to-wet weight conversions were not available so more general length-weight conversions for pteropods were applied based on those used by the GLOBal ocean ECosystems dynamics (GLOBEC) data management program. In GLOBEC, wet weights (WW) of different pteropod families were calculated based on their specific body geometry and length (Little and Copley, 2003). The GLOBEC conversions covered the barrel shaped *Clione* family of naked pteropods, the cone shaped family of *Styliola*, the low-spire (globular) family of *Limacina* spp., and the pyramidally shaped family of *Clio* spp. Accordingly, we assorted groups or species into respective geometric shapes and then applied the GLOBEC L to WW conversions. Although species-specific conversions are lacking for many of the groups (Table 2), we believe that this approach provides a reasonable first order approximation of individual biomass for the purpose of the present analysis. More specific details of these conversions are given below:

Equation (1) was used to convert all non-shelled (naked) taxa, including barrel-and oval- shaped families of *Spongiobranchia* spp., *Pneumodermopsis* and *Paedoclione* and class Gymnosomata (Little and Copley, 2003). Equation (2) was

Table 2. Length to weight equations for different pteropod groups based on the geometric shapes.

SPECIES	Group	Equation source	Conversion	Equation name	Equation (size-weight relationship)	Equation (Davis and Wiebe, 1985)	
Limacina helicina	Round/cylindrical/ globular	Bednaršek et al. (2012)	Diameter→DW		$DW = 0.137 \times D^{1.5005}$		
Limacina spp.	Round/cylindrical/ globular	GLOBEC	Diameter→DW		$WW = 0.000194 \times L^{2.5473}$	WW→DW	WW×0.28
Clione spp.	Barell/oval-shaped (naked)	GLOBEC	Length→WW	Pteropod (naked: Clione)	$WW = 10^{(2.533 \times \log(L) - 3.89095) \times 10^3}$	WW→DW	WW×0.28
Hyalocylis spp.	Cone/needle/ tube/bottle-shaped	GLOBEC	Length→WW	Pteropod (cone-shaped: Styliola)	$WW = PI \times L^{3 \times 3/25}$	WW→DW	WW×0.28
Styliola spp.	Cone/needle/ tube/bottle-shaped	GLOBEC	Length→WW	Pteropod (cone-shaped: Styliola)	$WW = PI \times L^{3 \times 3/25}$	WW→DW	WW×0.28
Spongiobranchaea spp.	Barell/oval-shaped (naked)	GLOBEC	Length→WW	Pteropod (naked: Clione)	$WW = 10^{(2.533 \times \log(L) - 3.89095) \times 10^3}$	WW→DW	WW×0.28
Pneumodermopsis and *Paedoclione*	Barell/oval-shaped (naked)	GLOBEC	Length→WW	Pteropod (naked: Clione)	$WW = 10^{(2.533 \times \log(L) - 3.89095) \times 10^3}$	WW→DW	WW×0.28
Cavolinia spp.	Triangular/ pyramidal	GLOBEC	Length→DW	Pteropod (Clio)	$WW = 0.2152 \times L^{2.293}$	WW→DW	WW×0.28
Clio spp.	Triangular/ pyramidal	GLOBEC	Length→WW	Pteropod (Clio)	$WW = 0.2152 \times L^{2.293}$	WW→DW	WW×0.28
Creseis spp.	Cone/needle/ tube/bottle-shaped	GLOBEC	Length→WW	Pteropod (cone-shaped: Styliola)	$WW = PI \times L^{3 \times 3/25}$	WW→DW	WW×0.28
Cuvierina spp.	Cone/needle/ tube/bottle-shaped	GLOBEC	Length→WW	Pteropod (cone-shaped: Styliola)	$WW = PI \times L^{3 \times 3/25}$	WW→DW	WW×0.28
Diacria spp.	Triangular/ pyramidal	GLOBEC	Length→WW	Pteropod (Clio)	$WW = 0.2152 \times L^{2.293}$	WW→DW	WW×0.28
Thecosomata	Shelled	Davis and Wiebe (1985)	Length→WW		$WW = 0.2152 \times L^{2.293}$	WW→DW	WW×0.28
Gymnosomata	Naked	Davis and Wiebe (1985)	Length→WW		$WW = 10^{(2.533 \times \log(L) - 3.89095) \times 10^3}$	WW→DW	WW×0.28
Pteropoda	Shelled	Davis and Wiebe (1985)	Length→WW		$WW = 0.2152 \times L^{2.293}$	WW→DW	WW×0.28

applied to *Clione* spp., being a genus species conversion equation originally derived by Böer et al. (2005):

$$WW = 10^{(2.533 \times \log(L) - 3.89095) \times 10^3}, \quad (1)$$

$$DW = 1.6146^{e0.0088 \times L}. \quad (2)$$

Three different shapes were distinguished within the shelled taxa, each with their own L to WW conversions:

$WW = WW = 0.2152 \times L^{2.293}$ triangular/pyramidal shaped (Davis and Wiebe, 1985) (3)

$WW = 0.000194 \times L^{2.5473}$ round/cylindrical/globular shaped (Little and Copley, 2003) (4)

$WW = PI \times L^{3 \times 3/25}$ cone/needle/bottle-shaped (Little and Copley, 2003). (5)

Limacinidae were one of the most abundant taxa within our database, for which there are several published L to DW conversions in the literature:

$$DW = 0.257L^{2.141} \text{ (Gannefors et al., 2005)} \quad (6)$$

$$\log DW = 0.685L^{-2.222} \text{ (Fabry, 1989)} \quad (7)$$

$$DW = 0.1365L^{1.501} \text{ (Bednaršek et al., 2012).} \quad (8)$$

Gannefors et al. (2005), Fabry (1989) and Bednaršek et al. (2012) fitted the respective functions to differing size ranges of *Limacinidae*, so we compared their performance across a uniform size range to consider their suitability for more broad scale application (Appendix B, Fig. B1). The functional form of Fabry (1989), although optimal for animals in a size range between 1 and 4 mm, became exponentially large at shell diameters above this range so was considered unsuitable for the present analysis. The Gannefors et

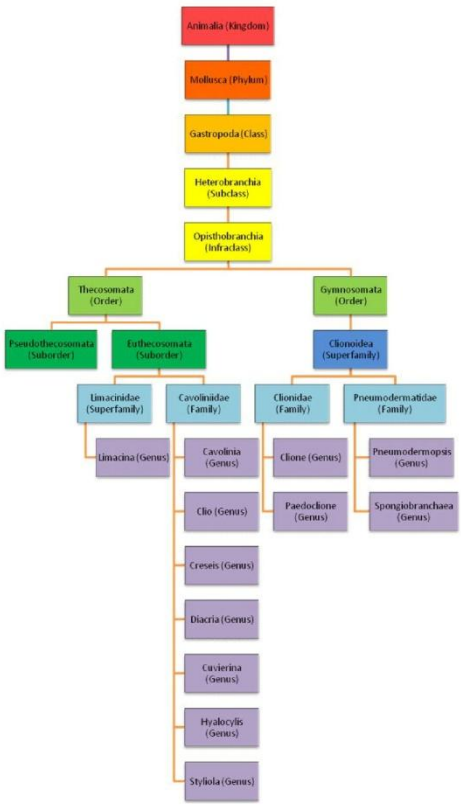

Figure 3. Taxonomy of pteropods.

al. (2005) and Bednaršek et al. (2012) functional forms performed similarly well and realistically (Appendix B) across the shell diameter size ranges encountered in the present study (0.01 to 50 mm). We chose the Bednaršek et al. (2012) function given that its estimate of dry weight between 1 and 4 mm shell diameter fell midway between the estimates of the Fabry (1989) and Gannefors et al. (2005) algorithms, combined with the fact that its behaviour remained realistic at larger size categories.

In cases, where the data-source referred to orders or classes rather than species, Eq. (3) was applied since the taxa were principally non-*Limacinidae* shelled species.

In the case of juveniles, the above length to weight conversions were used according to their respective taxa or body shape, but the length of the veligers and larvae set at 10 % of the adult average size, which is based on our own comparisons of average juvenile and adult sizes.

2.3.1 Calculation of length for the individual pteropod species

For some data records, only the species and abundance was recorded without any indication of individual size or weight. Individual shell diameter was therefore inferred in order to calculate biomass. Our first step was to determine size of adult specimens of each species using information from the Marine Species Identification Portal (http://species-identification.org/), of which results are presented in Appendix C (Table C1), along with the body shape, length and mean size.

Where the abundance data was given for a higher taxonomic level than species (e.g. class, suborder, order), the average length across all species within that respective taxa was determined (Table C1). Because this procedure only took account of adult sizes, we were aware that this would result in an overestimation of biomass. This was compensated for in two ways: firstly, by taking into account data points where a juvenile status was indicated (283 in total, representing 2 % of entire database) in which case length was assumed to be 10 % of adult size (see above). Secondly, where the data was not species-specific (but family- or higher order-specific), the average length across all species within the taxon was calculated, so preventing extreme bias from very large or very small species.

Unfortunately, the lack of data points where both biomass and abundance values were reported made it impossible to do a quantitative comparison of the performance of our L to W conversions.

2.3.2 Calculation of dry weight and carbon biomass from wet weight

Wet weight was converted to dry weight using Davis and Wiebe (1985):

$$DW = WW \times 0.28. \quad (9)$$

Biomass was subsequently transformed to carbon using a conversion factor of 0.25, following Larson (1986).

2.3.3 Global contribution of shelled pteropods to carbonate biomass

Once conversions from abundance to carbon biomass had been completed, we considered the global biomass distribution of both shelled and non-shelled pteropod taxa. Separating out the shelled pteropod taxa allows the global carbonate distribution resulting from pteropods to be assessed, so permitting the evaluation of their contribution to the global carbonate budget. Bednaršek et al. (2012) have calculated inorganic carbon as a percentage of total organic subtracted from total carbon, deducing the PIC/POC ratio of 0.27 vs. 0.73.

Table 3. Mean, median, maximum and minimum and standard deviation (SD) of pteropod biomass (mg C m^{-3}) determined (i) for all global data, (ii) all non-zero data points, (iii) all non-zero Northern Hemisphere (NH) data-points and (iv) all non-zero Southern Hemisphere (SH) data-points.

summed biomass data	mean	median	max	min	SD
all global data	4.09	0.008	5.05e+003	0.00	59.06
non-zero global data	4.58	0.0145	5.05e+003	1.00e-006	62.46
for the NH non-zero data	4.04	0.0145	5.05e+003	1.00e-006	64.84
for the SH non-zero data	8.15	0.001	608.35	2.00e-006	45.36

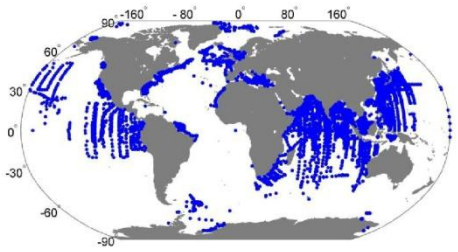

Figure 4. Global distribution of quality-controlled pteropod data.

Assuming that all inorganic carbon is in the form of calcium carbonate, the amount of calcium carbonate can be estimated as follows:

$$CaCO_3\ (\%) = [TC\ (\%) - TOC\ (\%)] \times 8.33 \quad (10)$$

where the constant 8.33 represents the molecular mass ratio of carbon to calcium carbonate.

3 Results

3.1 Global data distribution of biomass data

Altogether, we collected 25 939 data entries across all oceanic regions, which corresponded to 15 134 samples of total pteropod biomass (Fig. 4). Out of these, 14 136 data points (93 %) represented shelled pteropods (Thecosomes), and the remaining 7 % represented non-shelled pteropods (Gymnosomes). Within the whole data set, 1608 data points (11 % of all values) were reported as zero values for all pteropod groups.

Although pteropod observations were available for all ocean basins, there was a clear bias of the data towards observations in the Northern Hemisphere (NH) (77 % of non-zero entries), with the remaining 23 % in the Southern Hemisphere (SH, Table 3 and 6, Fig. 4). With respect to latitude, the most entries (37 %) were collected within the latitudinal band of 10–60° N (Table 4).

The maximum net sampling depth was 2000 m but 83 % of all nets were sampled to a maximum depth of 200 m (Table 5). Across all observations, 62 % of all biomass occurred within the top 200 m, with the remaining biomass (38 %) being relatively evenly distributed down to 2000 m. The deepest occurrence of pteropods in our database was 2000 m, located at 81° N,163° E. The highest biomass for shelled pteropods (2980 mg C m^{-3}) was recorded at the surface in the NH temperate region, at 42° N,70° W. The highest biomass for the non-shelled pteropods (5045 mg C m^{-3}) was recorded in the same region (42° N,66° W). There were very few direct measurements of pteropod biomass (see Sect. 2.3), but of those, the highest recorded values were in the Sea of Okhotsk (54° N,138° E), where biomass reached 538 mg C m^{-3} (Rogachev et al., 2008).

3.2 The effect of nets and mesh sizes on global pteropod biomass

Mesh size will influence the size range of organisms captured by nets. In assembling this database, we decided to include all net-catch data, irrespective of mesh size. This will undoubtedly create error, particularly in the undersampling of smaller individuals by larger meshed nets through the lack of retention and of larger, more motile individuals by finer meshed nets through avoidance. For the purpose of the present analysis, with a focus mainly on comparative patterns, it is important that these errors do not generate bias, since this could distort any discerned geographic trends. We considered this in two ways. In Fig. 1, we compared the biomass to net mesh size across 19 671 samples. The figure shows a peak in biomass towards the mid-size meshes (~ 300 µm). This demonstrates that the majority of biomass lay within organisms with an equivalent spherical diameter of 300 µm or greater, and that the undersampling of smaller organisms by some studies is unlikely to have a considerable impact on biomass estimates. Equally, the figure is indicating that the average biomass is similar, regardless of the mesh size used for sampling.

In Fig. 2, net mesh-size was compared to latitude. Although this illustrates the considerable variety of meshes used within the present database, it also shows there was no apparent bias towards certain mesh size being used at some latitudes more than others. Therefore, although the use of different meshes between studies is undoubtedly a source of

Table 4. Latitudinal distribution of abundance data in ten degree latitudinal bands (90° to 90°). Mean, maximum (max), median and standard deviation (SD) of biomass (mg C m^{-3}) per latitudinal band, calculated from non-zero data points.

Latitude	Entries	Mean (mg C m^{-3})	SD	Max (mg C m^{-3})	Min (mg C m^{-3})	Median (mg C m^{-3})
90 to 80° S	0	–	–	–	–	–
80 to 70° S	72	27.20	98.44	557.41	0.001	0.19
70 to 60° S	59	0.09	0.42	2.63	2.00e-006	0
60 to 50° S	90	13.93	35.55	168.47	0.01	0.48
50 to 40° S	90	0.25	2.27	21.53	8.00e-006	1.32e-004
40 to 30° S	127	0.02	0.07	0.64	2.83e-006	8.80-005
30 to 20° S	167	0.01	0.05	0.45	5.33e-006	2.18e-004
20 to 10° S	310	0.02	0.08	0.86	3.25e-006	6.14e-004
10° N to 0°	1007	11.93	53.98	608.35	3.50e-006	0
0° to 10° N	1078	0.06	0.26	4.30	4.67e-006	0.01
10° to 20° N	2044	1.47	8.91	226.66	1.00e-006	0.01
20° to 30° N	1725	0.06	0.49	9.85	8.00e-006	0.003
30° to 40° N	2958	4.51	21.65	362.89	1.00e-006	0.01
40° to 50° N	744	34.76	248.13	5.05e+003	2.90e-005	0.09
50° to 60° N	1960	1.26	17.26	538	0.003	0.40
60° to 70° N	896	0.31	0.46	11.82	0.003	026
70° to 80° N	77	17.31	61.97	517.05	1.75e-004	0.69
80° to 90° N	177	4.60	10.63	34.33	1.00e-006	0.01

Table 5. Depth distribution of non-zero biomass values. Mean, maximum (max), median and standard deviation (SD) of biomass (mg C m^{-3}) per depth interval, calculated from non-zero data points.

depth range (m)	entries	Mean (mg C m^{-3})	Max (mg C m^{-3})	Min (mg C m^{-3})	Median (mg C m^{-3})	SD
0–10	1806	20.65	5.45e+003	0	0.02	157.81
10–25	612	14.44	557.41	0	0.04	57.53
25–50	1296	3.25	434.37	0	0.002	18.26
50–200	7508	0.65	308.47	0	0.02	5.74
200–500	2028	0.19	9.85	0	0.002	1.04
500–2000	276	0.02	3.20	0	0.004	0.18

error, it is not a major source of bias in our analyses of geographic trends in pteropod biomass distribution.

3.3 Temporal distribution of data

Our database spans the period 1950–2010, and temporally, the data was fairly evenly distributed across all decades, with at least one sampling peak per decade. Several sampling peaks were recorded in the late 1950s, then in the 1960s–1970s, followed by high numbers of data from the early 1990s and 2000s. We recorded fewer samples in the 1980s (Fig. 6). To check for seasonal biases, the data was divided into four seasons for each hemisphere (Table 7). While in the NH, the data was distributed evenly across the four seasons (24 % in 335 spring, 23 % in summer, 24 % in autumn and 30 % in winter), sampling in the SH was biased towards winter and summer (30 % and 25 %, respectively), with much lower coverage during the other seasons (19 and 16 % in spring and fall, respectively).

3.4 Global biomass characteristics for all pteropod groups and for shelled-pteropods only

For all pteropod groups combined, the range of global biomass concentrations was wide, spanning over four orders of magnitude (Fig. 8a), with a mean and median biomass of 4.1 mg C m^{-3} (SD = 59.1) and 0.0083 mg C m^{-3} for all data points, and 4.6 mg C m^{-3} (SD = 62.5) and 0.0145 mg C m^{-3} for non-zero biomass values, respectively. In the NH, the mean biomass was 4.0 mg C m^{-3} (SD = 64.8) and the median biomass, 0.02 mg C m^{-3}. In the SH, the mean biomass was 8.15 mg C m^{-3} (SD = 45.4) and the median biomass 0.001 mg C m^{-3} (Table 3). Although the median biomass in the SH was one order of magnitude smaller than in the NH, the mean biomass in the SH was twice that of the NH.

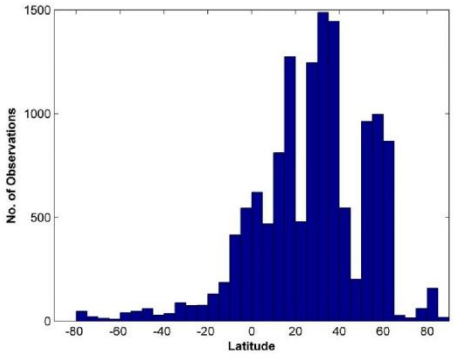

Figure 5. Number of pteropod observations as a function of latitude for the period 1950–2010.

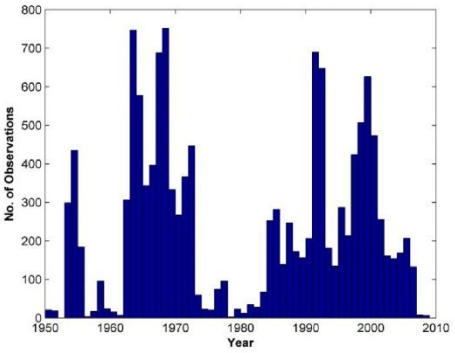

Figure 6. Number of observations per year, for the years 1950–2010.

For shelled pteropod groups only, the mean and median biomass for non-zero values was 3.81 mg C m^{-3} (SD = 40.24), and 0.0078 mg C m^{-3}, respectively, and the maximum biomass was 2979.7 mg C m^{-3}. Considering the mean biomass of shelled and non-shelled pteropods, shelled pteropods constitute 83 % to the total pteropod biomass, the remainder being made up of non-shelled pteropod taxa. When considered in terms of median biomass, 54 % was made up of shelled-pteropods and 46 % made up of non-shelled pteropods, indicating that the dominance of shelled-pteropods is in part due to the fact that they sometimes occur at very high concentrations.

Through assuming, firstly, an inorganic to organic carbon ratio of 0.27 : 0.73 (Bednaršek et al., 2012) and secondly an inorganic carbon to calcium carbonate molecular mass ratio of 8.33 (Eq. 10) gave a mean global carbonate biomass of 23.17 mg $CaCO_3$ m^{-3}, and a maximum biomass was 1.81 g $CaCO_3$ m^{-3}. These estimates were derived from non-zero biomass records only.

Table 6. Percentage distribution of non-zero data entries with respect to month for the Northern (NH) and Southern (SH) Hemispheres.

months	entries	NH season	SH season	% NH non-zero data	% SH non-zero data
January	1185	winter	summer	8.4	11.7
February	1457	winter	summer	9.4	20.7
March	998	spring	autumn	7.4	6.1
April	1298	spring	autumn	9.5	9.0
May	876	spring	autumn	6.9	3.7
June	802	summer	winter	6.4	4.1
July	1352	summer	winter	10.4	7.1
August	1790	summer	winter	13.1	13.8
September	1143	autumn	spring	8.4	9.0
October	1049	autumn	spring	8.4	3.7
November	859	autumn	spring	6.8	3.7
December	806	winter	summer	5.4	10.2

3.4.1 Latitudinal biomass distribution

Pteropods were found at all latitudes at which samples were taken (Figs. 5, 8a). The highest maximum, mean and median biomass values were located in the NH between 40 and 50° N (mean biomass of 5.42 mg C m^{-3} (SD = 79.94), median biomass of 0.06 mg C m^{-3}). The highest mean and median biomass values in the SH were located between 70 and 80° S (39.71 mg C m^{-3} (SD = 93.00) and 0.009 mg C m^{-3}, respectively; Table 3). However, relatively high biomasses were not restricted to a particular latitude or ocean basin but were widespread, including high-latitudinal, temporal and equatorial regions in the both hemispheres. The only exception was the latitudinal band between 20 and 40° in the NH and SH, where biomass was considerably lower (Fig. 8). There was a difference in latitudinal trends between hemispheres (Fig. 9a, b), with highest biomass values in the NH being at mid-latitudes decreasing towards the equator and the poles, while, in the SH, highest biomass values were seen at the poles and steadily decreasing through the mid-latitudes towards the equator. Biomass values at both poles were within the same order of magnitude.

3.4.2 Depth distribution

Pteropods were observed at all depths down to 2000 m, although the funnel-shaped biomass pattern from the surface towards the depth indicates a sharp decrease in biomass below 200 m (Fig. 8b). The highest values were recorded at the surface (0–10 m), with a mean biomass of 20.65 mg C m^{-3} (SD = 157.81) and median biomass of 0.02 mg C m^{-3}. Mean

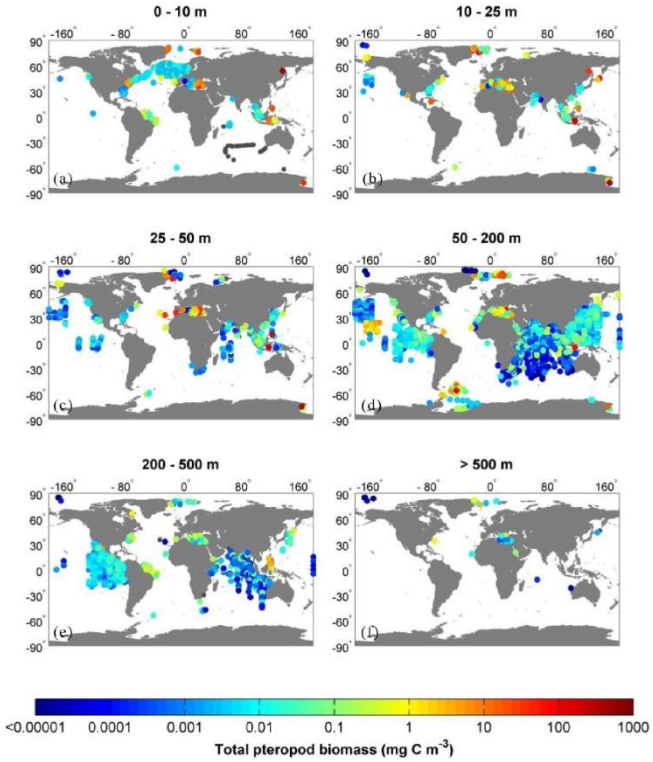

Figure 7. Pteropod carbon biomass (mg C m^{-3}) for six depth intervals: **(a)** surface (0–10 m), **(b)** 10–25 m, **(c)** 25–50 m, **(d)** 50–200 m, **(e)** 200–500 m, **(f)** ≥ 500 m.

and median biomass gradually decrease with the depth by one order of magnitude from 10 to 200 m, and by two orders of magnitude between the 10–200 m and 200–2000 m depth bands (Table 5, Fig. 8b).

The pattern of pteropod distribution demonstrates that higher abundances are closely related to continental shelves and areas of high productivity or nutrient loads (Fig. 7). This can be particularly exemplified in the eastern North Pacific central water, which is a rather small area affected by the inflow from the more productive transitional and equatorial adjacent areas (Longhurst, 2007), with a three to four magnitude higher biomass, in comparison to the surrounding areas.

In all ocean basins, biomass levels above 100 mg C m^{-3} only occurred in the 0–200 m depth layers. However, in tropical regions, some of the highest biomass levels were found in the 200–500 m depth strata, where concentrations typically reached between 1 and 10 mg C m^{-3} (Fig. 7). This suggests that tropical species concentrate at deeper depths than temperate and high-latitude species. Such geographic patterns in the depth distribution of pteropods have previously been noted by Solis and von Westernhagen (1978), Wormuth (1981) and Almogi-Labin et al. (1998).

3.4.3 Seasonal distribution of pteropod biomass

Seasonal variations in biomass values were much more extreme in the SH compared to the NH, although it is to be noted that sample coverage was comparatively greater in the NH (Table 7, Fig. 9). In both hemispheres, mean biomass peaked in the spring. However, the peak was an order of magnitude higher in the SH compared to the NH (Table 7). The ratio between spring and winter biomass was approximately 2 : 1 in the NH, but around 1300 : 1 in the SH. The difference in ratios is mainly explained by the virtual disappearance of

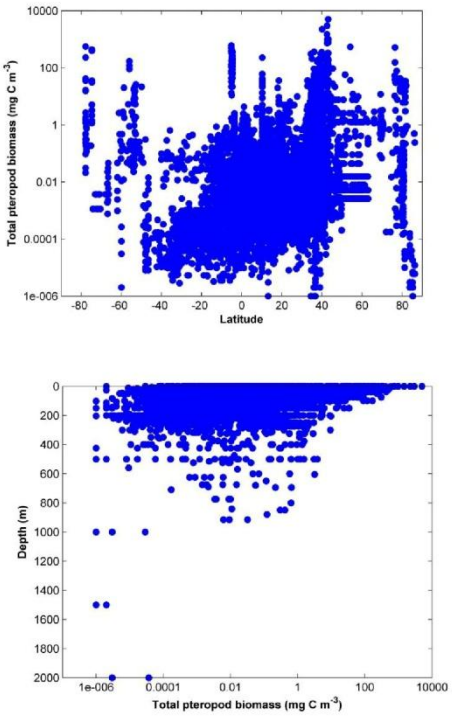

Figure 8. (Above) the distribution of pteropod biomass (mg C m^{-3}) as a function of latitude; (below) the relationship between pteropod biomass and net-capture depth.

pteropods in the SH during winter. Biomass levels were relatively similar between the NH and SH during summer and autumn. The seasonal peaks and troughs in mean biomass in both hemispheres correspond to a life-history pattern of spring spawning, probably in response to seasonal pulses of productivity, as described by Hunt et al. (2008) and Bednaršek et al. (2012).

Despite the seasonal peaks and troughs in biomass, a residual biomass level was always present (Fig. 9). This indicates that there must be a degree of overlap in generations (Bednaršek et al., 2012). In the higher latitudes, where there is likely just a single recruitment event per year, meaning that these pteropods must have a life-cycle that extends into a second year. In the Southern Ocean, Bednaršek et al. (2012) proposed that some *Limacina helicina ant.* lived for more than 2 yr and, although small in number, these individuals may be vital for future recruitment. Strong seasonality increases the vulnerability of early life-stages of pteropods that rely on pulses of production to thrive (Bernard and Froneman, 2009; Seibel and Dierssen, 2003). An overlap of generations gives populations greater stability in temporally variable environments.

3.4.4 Global estimates of the pteropod biomass stock and productivity

Given representative data coverage at the both hemispheres, global mean pteropod biomass of 0.0046 g C m^{-3} (SD = 62.5) was calculated for any point of time. To extrapolate from regional to global pteropod biomass, pteropod depth distribution and absolute area of the global ocean are required. With regards to depth distribution, Fig. 8a is indicative of pteropod biomass to be uniformly distributed within the upper 300 m, and two orders of magnitude less abundant below 300 m. The 300-m depth level was hence taken as a conservative estimate of their overall occurrence. Considering the absolute surface area of the global deep ocean (Milliman and Droxler, 1996; total area equals 362.03×10^6 km^2 cf. Dietrich et al., 1975), two values were taken to determine global pteropod biomass: the global ocean surface excluding shelf seas (322×10^6 km^2) was taken as a minimum area inhibited by pteropods, while the total ocean surface area was determined as a maximum (362.03×10^6 km^2). Considering minimum and maximum area inhabited by pteropods, global pteropod biomass ranges from 444 to 505 Tg of C at any point in time. This range of estimates, based on the observational results is similar to pteropod productivity estimate of 0.87 Pg C yr^{-1} obtained through modelling work by Gangstø et al. (2008). Lebrato et al. (2010) estimated global carbon productivity budget to range between 0.96 and 2.56 Pg C yr^{-1}. This indicates that pteropods contribute 20–42 % towards global carbonate budget.

The average turnover time is known to be different for various species, shorter (several months) for tropical species and longer (more than one year) for the high-latitudinal species (Lalli and Gilmer, 1989). Here, as reported in several papers (Van der Spoel, 1973; Wells Jr., 1976; Hunt et al., 2008; etc.), the average pteropods turnover time was assumed to be one year, with high latitudinal species to be exceptions (e.g. Bednaršek et al., 2012) and recorded the life cycle of *Limacina helicina antarctica* to span over 3 yr. At a global scale, and an average annual distribution, the entire pteropod production would hence amount to 444–505 Tg C yr^{-1}, which is about five times the estimated planktic foraminifers biomass production (Schiebel and Movellan, 2012: 25–100 Tg C yr^{-1}), more than double of the estimated diazotroph biomass (Luo et al., 2012: 40–200 Tg C), and around one fifth of the total diatom production (Leblanc et al., 2012: 500–3000 Tg C). Comparing global pteropod to coccolithophorid carbon productivity (Balch et al., 2007), coccolithophorid production are approximately 1.5 to 3 times higher than our estimated pteropod production.

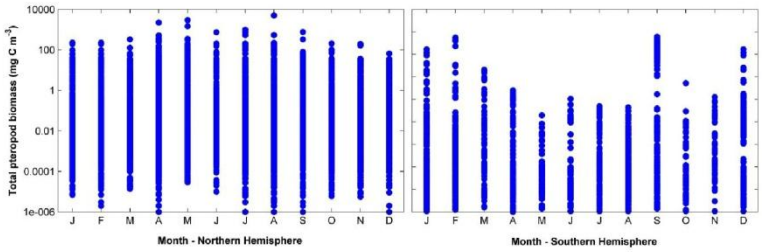

Figure 9. Distribution of pteropod biomass values (mg C m^{-3}) with respect to month, in the Northern Hemisphere (left) and Southern Hemisphere (right).

Table 7. Biomass (mg C m^{-3}) with respect to season for the Northern (NH) and Southern (SH) Hemispheres, showing the calculated mean, standard deviation (SD), median, minimum (min) and maximum (max). Biomass statistics are based on non-zero data entries only.

	NH mean	NH SD	NH median	NH min	NH max	SH mean	SH SD	SH median	SH min	SH max
winter	2.77	15.63	0.02	1e-006	557.41	0.03	0.09	4.54e-004	2.00e-006	1.06
spring	5.42	79.94	0.06	1e-006	3.0e+003	39.71	93.00	0.009	7.50e-006	608.35
summer	4.32	92.69	0.02	1e-006	5.05e+003	3.73	32.83	0.002	3.00e-006	557.41
autumn	2.44	18.39	0.03	1e-006	765.24	0.51	2.47	7.28e-004	3.30e-006	21.05

4 Discussion and conclusions

The aim of this study was to collect and synthesise available existing abundance and biomass data to generate the first global pteropod biomass database. Most studies reported abundance rather than biomass data, making it necessary to estimate carbon biomass using length to weight conversions and introducing levels of uncertainty as a result. Further uncertainties in the biomass estimates in this study will result from sampling errors such as net-escapement and net-avoidance, the variation in size classes between different pteropod species and generations. Further considerations around these uncertainties are discussed below.

With regards to the sampling error, the use of different nets for different pteropod size classes generates uncertainty, as the capture and filtering efficiencies differ between nets. Furthermore, sampling issues such as net-avoidance behaviour, extrusion of animals through mesh and clogging of the net (Harris et al., 2000) will influence abundance measurements. In addition, there is generally an insufficient use of smaller meshed nets to estimate population size. Wells Jr. (1973) proposed that there was a clear underestimation of the fraction of the pteropod population smaller than 100 µm. As they constitute by far the most numerous part of the natural population (Fabry, 1989), there is a clear under-representation of this cohort in the scientific literature and thus of their importance within the microzooplankton community (Dadon and Masello, 1999). When sampling with small vertical nets, which preferentially catch small or sluggish taxa, additional sampling errors arise from the fact that the nets can be avoided by larger plankton. On the other hand, nets with larger mesh size can miss the mesozooplankton size fractions including pteropods (Boysen-Ennen et al., 1991). We tried to address potential biases through systematic examination of mesh sizes, net types and sampling strategies (wherever available in the literature) relative to biomass estimates. Our analyses indicated, firstly, that most biomass lay within the mid-size ranges, meaning that the undersampling of smaller organisms by some studies is unlikely to have a large impact on biomass estimates. Secondly, there was no geographic bias in the use of different nets and meshes, indicating that sampling error is unlikely to bias analyses of geographic trends in biomass. Overall, we conclude that the documented variation in mesh size between studies included within the database was not a source of a large-scale bias within global biomass patterns. Therefore, although users of the database must be vigilant with regards to this potential source of error, we believe that the inclusion of all data, irrespective of the mesh size and sampling strategy used, maximises the potential insights that can be gained from this database.

There were a number of sources of uncertainty in deriving biomass values from the majority of studies within the database that only provided abundance data. To convert from abundance to biomass requires knowledge of the length distribution of specimens but neither this data, nor the respective life-stages of specimens were commonly reported. Where such information was not given, we assumed that all specimens were adults and used literature based estimated of body

length. This approach probably resulted in an overestimation of biomass, given that at least part of the sampled population may have been smaller juvenile stages. Furthermore, where sizes were reported, there was often a lack of further statistical descriptors such as minimum or maximum length, so preventing levels of variance in biomass to be estimated. For some species, there was no available length to weight conversions and so more generic algorithms were applied based on the shape and morphological features (shelled/non-shelled) of the organisms, following the approach of GLOBEC (Little and Copley, 2003). This approach no doubt introduced further errors although there is little alternative to the use of such generic functions until a more systematic documentation of the length and weight characteristics of a wider range of pteropod species is undertaken.

The seasonal spread of sampling was much more even in the NH compared to the SH. Whereas we were able to document how patterns of biomass shifted geographically between seasons in the NH, our ability to achieve this was far more constrained in the SH. In particular, sampling in winter and spring was particularly sparse in the SH. It is important that future sampling efforts in that hemisphere concentrate on these less sampled times of year.

This study has enabled estimates of global pteropod biomass across a number of spatial and temporal scales. Furthermore, it has revealed some global patterns of pteropod biomass, only possible due to the wealth of data available in our data sets. Also, calculating the biomass of shelled pteropods only, we have estimated the contribution of this group to the global carbonate inventory. This database has the potential be a valuable tool for future modelling work, both of ecosystem processes and for the study of global biogeochemical cycles, since pteropods are a major contributor to organic and inorganic carbon fluxes. It can also make a timely contribution to the assessment of the effects of ocean acidification, particularly in terms of the vulnerability of calcifying species, since it provides a benchmark against which model projections and future sampling efforts can be compared.

Appendix A

A1 Available dataset at PANGEA

A full data set containing all abundance/biomass data points can be downloaded from the data archive PANGAEA, The data file contains longitude, latitude, sampling depth (m), date (Year, Month, Day in ISO format), taxon/species/body size, abundance (ind. m^{-3}), biomass (C mg m^{-3}), mesh size (μm), sampling strategy and full data reference list (doi/journal/database) doi:10.1594/PANGAEA.777387.

A2 Gridded NetCDF biomass product

The biomass data has been gridded onto a $360 \times 180°$ grid, with a vertical resolution of 33 WOA depth levels. Data has been converted to NetCDF format for easy use in model evaluation exercises. The NetCDF file can be downloaded from PANGAEA (doi:10.1594/PANGAEA.777387). It contains data on longitude, latitude, sampling depth (m), month, abundance (ind. m^{-3}) and biomass (mg C m^{-3}).

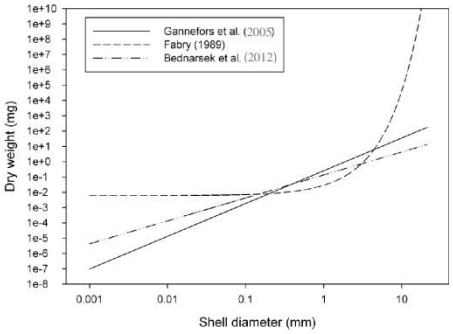

Figure B1. Shell diameter to dry weight relationships for *Limacina helicina* derived by three different studies.

Table C1. Body dimensions and shapes of a range of shelled and non-shelled pteropod species (source: Marine identification portal (http://species-identification.org/), except for *Clione limacina** – Böer et al., 2005).

Order	Suborder	Taxon	Subspecies/ Formae	Mean shell length (mm)	Mean shell width (mm)	Body length (mm)	Shell/body shape	Additional information	Group
Thecosomata	Euthecosomata	*Limacina helicina*	*helicina helicina*	6	8		round	left coiled shell, moderately highly spired, aperture higher than wide, height/diameter ration=0.75	Round/cylindrical/ globular
Thecosomata	Euthecosomata	*Limacina helicina*	*helicina pacifica*	5	2				Round/cylindrical/ globular
Thecosomata	Euthecosomata	*Limacina retroversa*	*retroversa*	2.5	2.6		round	small, left coiled shell, no umbilical keel, spire moderately highly coiled	Round/cylindrical/ globular
Thecosomata	Euthecosomata	*Limacina bulimoides*		2	1.4		round	highly coiled spire	Round/cylindrical/ globular
Thecosomata	Euthecosomata	*Limacina inflata*			1.3		round	coiled nearly in one level; average shell diameter =0.86, aperture length=0.68 mm, diameter of operculum=0.31 mm, aperture breadth=0.5 mm	Round/cylindrical/ globular
Thecosomata	Euthecosomata	*Limacina helicina*	*antarctica*		5		round	left coiled, spire variable	Round/cylindrical/ globular
Thecosomata	Euthecosomata	*Limacina helicina*	*antarctica antarctica rangii*	2	3.5				Round/cylindrical/ globular
Thecosomata	Euthecosomata	*Limacina trochiformis*		1	0.8		round	left coiled, apical angle 75–96°	Round/cylindrical/ globular
Thecosomata	Euthecosomata	*Limacina helicina* spp. *average*			4.22				Round/cylindrical/ globular
Thecosomata	Euthecosomata	*Limacina trochiformis*		1	0.8		round	left coiled, apical angle 75–96°	Round/cylindrical/ globular
Thecosomata	Euthecosomata	*Limacina lesueuri*		0.8	1		round	flatly left coiled, spire depressed; max diameter of operculum = 0.6 mm and length/width ratio=2/3	Round/cylindrical/ globular
Thecosomata	Euthecosomata	*Limacina* spp.			2.98			the length calculated as the average of all species	Round/cylindrical/ globular
Gymnosomata		*Clione limacina*	*limacina antarctica*		25	Up to 40	barrel	body pointed posteriorly	Barrel/oval-shaped (naked)
Gymnosomata		*Clione limacina*	*limacina meridionalis*		21	20	barrel	Cone elongated	Barrel/oval-shaped (naked)
Gymnosomata		*Clione limacina**			12				Barrel/oval-shaped (naked)
Gymnosomata		*Clione limacina larvae*			0.3				
Gymnosomata		*Clione* spp.			14.57			the length calculated as the average of all species	Barrel/oval-shaped (naked)
Thecosomata	Euthecosomata	*Hyalocylis striata*		8		up to 8	cylindrical	uncoiled, cross-section round, shell curved faintly dorsally; rear angle of adult shell 24°	Cone-shaped (needle/tube/bottle)

Table C1. Continued.

Order	Suborder	Taxon	Subspecies/ Formae	Mean shell length (mm)	Mean shell width (mm)	Body length (mm)	Shell/body shape	Additional information	Group
Thecosomata	Euthecosomata	*Styliola subula*		13		13	needle-like	shell is (conical), uncoiled, the cross-section is round, long, tubular, not curved; rear angle of shell is 11°	Cone-shaped (needle/tube/bottle)
Gymnosomata		*Spongiobranchaea australis*		20		max 22	oval	long body	Barrel/oval-shaped (naked)
Gymnosomata		*Spongiobrachaea australis juv.*		10					Barrel/oval-shaped (naked)
Gymnosomata		*Spongiobranchaea* spp.		15					Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*teschi*			up to 9.1	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*pulex*			up to 8	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*macrochira*			up to 2	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*ciliata*			up to 15	barrel	slender body	Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*spoeli*			up to 3 (2.6)	barrel	body rounded then contracted	Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*simplex*			up to 5 (4.5)	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*paucidens*			up to 5	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*canephora*			up to 12	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis*	*polycotyla*			up to 5	barrel		Barrel/oval-shaped (naked)
Gymnosomata		*Pneumodermopsis* spp.				6.5		the length calculated as the average of all species	Barrel/oval-shaped (naked)
Gymnosomata		*Paedocline*	*doliiformis*	1.5				elongate oval to cylindrical shape	Barrel/oval-shaped (naked
Thecosomata	Euthecosomata	*Cavolinia globulosa*		6	4.5		globular		Triangular/pyramidal
Thecosomata	Euthecosomata	*Cavolinia inflexa*	*inflexa*	7	5	6	triangular		Triangular/pyramidal
Thecosomata	Euthecosomata	*Cavolinia inflexa*	*imitans*	8			triangular		Triangular/pyramidal
Thecosomata	Euthecosomata	*Cavolinia inflexa*	*labiata*	8	5.5		triangular		Triangular/pyramidal
Thecosomata	Euthecosomata	*Cavolinia longirostris*	*f. longirostris*	6.2	6.8–4.9	7	triangular	accepted name *Dicavolinia longirostris*	Triangular/pyramidal
Thecosomata	Euthecosomata	*Cavolinia longirostris*	*f. angulosa*	3.9	3.7–2.3	5	triangular	accepted name *Dicavolinia longirostris*	Triangular/pyramidal
Thecosomata	Euthecosomata	*Cavolinia longirostris*	*f. strangulata*	4	4.1–2.7	5	triangular	accepted name *Dicavolinia longirostris*	Triangular/pyramidal
Thecosomata	Euthecosomata	*Cavolinia uncinata*	*uncinata uncinata*	6.5	4.0–6.6	8	triangular	uncoiled shell	Triangular/pyramidal
Thecosomata	Euthecosomata	*Cavolinia uncinata*	*uncinata f. pulsatapusilla*	6.1	9.5		triangular		Triangular/pyramidal
Thecosomata	Euthecosomata	*Cavolinia* spp.		6.2				the length calculated as the average of all species	Triangular/pyramidal
Thecosomata	Euthecosomata	*Clio convexa*		8	4.5	up to 8	pyramidal	shell uncoiled	Triangular/pyramidal

Table C1. Continued.

Order	Suborder	Taxon	Subspecies/ Formae	Mean shell length (mm)	Mean shell width (mm)	Body length (mm)	Shell/body shape	Additional information	Group
Thecosomata	Euthecosomata	*Clio cuspidata*		20	30	up to 20	pyramidal	shell uncoiled	Triangular/pyramidal
Thecosomata	Euthecosomata	*Clio piatkowskii*		13.5	16	14	broad pyramidal		Triangular/pyramidal
Thecosomata	Euthecosomata	*Clio pyramidata*		20	10		pyramidal		Triangular/pyramidal
Thecosomata	Euthecosomata	*Clio pyramidata*	*martensi*	17					Triangular/pyramidal
Thecosomata	Euthecosomata	*Clio pyramidata*	*antarctica*	17					Triangular/pyramidal
Thecosomata	Euthecosomata	*Clio pyramidata*	*lanceolata*	20					Triangular/pyramidal
Thecosomata	Euthecosomata	*Clio pyramidata* spp.		18.5					Triangular/pyramidal
Thecosomata	Euthecosomata	*Clio* spp.		16.5				the length calculated as the average of all species	Triangular/pyramidal
Thecosomata	Euthecosomata	*Creseis acicula*	*acicula*	33	1.5		tube	shell is not curved, cross-section circular, extremely long and narrow, aperture rounded, rear angle of shell 13–14°	Cone-shaped (+needle/ tube/bottle)
Thecosomata	Euthecosomata	*Creseis acicula*	*clava*	6					Cone-shaped (+needle/ tube/bottle)
Thecosomata	Euthecosomata	*Creseis acicula* spp.		19.5					Cone-shaped (+needle/ tube/bottle)
Thecosomata	Euthecosomata	*Creseis virgula*	*virgula*	6	max 2	6	tube	shell is curved (distinctly curved dorsally), uncoiled, long and narrow	Cone-shaped (+needle/ tube/bottle)
Thecosomata	Euthecosomata	*Creseis virgula*	*conica*	7	aperture-diameter =1 mm	up to 7	tube	shell curved and slender, cross-section is round	Cone-shaped (+needle/ tube/bottle)
Thecosomata	Euthecosomata	*Creseis virgula*	*constricta*	3.5	0.4	4	tube	uncoiled shell, cross-section round, short and narrow, slightly curved	Cone-shaped (+needle/ tube/bottle)
Thecosomata	Euthecosomata	*Creseis virgula* spp.		5.5	0.2		tube		Cone-shaped (+needle/ tube/bottle)
Thecosomata	Euthecosomata	*Creseis* spp.		11.5				the length calculated as the average of all species	Cone-shaped (+needle/ tube/bottle)
Thecosomata	Euthecosomata	*Cuvierina columnella*	*columnella*	10	3	up to 10	bottle-shaped	the greatest shell width is found at less than 1/3 of the shell length from posterior	Cone-shaped (+needle/ tube/bottle)
Thecosomata	Euthecosomata	*Diacria costata*		2.3	1.7–2.2	3	globular	shell uncoiled	Triangular/pyramidal
Thecosomata	Euthecosomata	*Diacria danae*		1.7	1.1–1.7	2	globular	shell uncoiled	Triangular/pyramidal
Thecosomata	Euthecosomata	*Diacria quadridentata*		3	1.8–2.5	2	globular	shell uncoiled	Triangular/pyramidal

Table C1. Continued.

Order	Suborder	Taxon	Subspecies/ Formae	Mean shell length (mm)	Mean shell width (mm)	Body length (mm)	Shell/body shape	Additional information	Group
Thecosomata	Euthecosomata	*Diacria rampali*		9.5	9	9	cone-shaped	bilateral symmetrical, uncoiled shell, slender, long caudal spine; spine mark width=0.95 mm, aperture height=0.95.	Triangular/pyramidal
Thecosomata	Euthecosomata	*Diacria trispinosa*	*trispinosa*	8	10	1	cone-shaped	bilateral symmetrical, uncoiled shell, long caudal spine; the ration upperlip-spine tip/spine tip-membrane=1.3, spine mark width=1.5 mm, aperture height=0.9 mm.	Triangular/pyramidal
Thecosomata	Euthecosomata	*Diacria major*		10.7	11			uncoiled bilateral symmetrical, long caudal spine; ratio upperlip-spine tip/spine-tip membrane=1,.65 mm, spine mark width=1.2 mm, aperture height=1 mm;	Triangular/pyramidal
Thecosomata	Euthecosomata	*Diacria* spp.		5.9				the length calculated as the average of all species	Triangular/pyramidal
THECOSOMATA COMBINED				8.1				shelled	
GYMNOSOMATA COMBINED						12.0		naked	
PTEROPODA COMBINED				8.9				shelled	

Acknowledgements. We thank K. Blachowiak-Samolyk, E. Boysen-Ennen, E. A. Broughton, C. Clarke, M. Daase, V. G. Dvoretsky, T. D. Elliot, H. Flores, B. A. Foster, P. W. Froneman, B. P. V. Hunt, L. Mousseau, J. Nishikawa, M. D. Ohman, T. O'Brien, E. A. Pakhomov, L. Pane, M. Fernandez de Puelles, K. A. Rogachev, P. H. Schalk, N. Solis, K. M. Swadling, A. F. Volkov, P. Ward, I. Werner, J. H. Wormuth for a permission to use and republish their data on pteropods in the MAREDAT project and this paper.

The lead author is grateful to R. A. Feely (NOAA) and R. Schiebel (Université d'Angers-BIAF) for their invaluable advice and ideas. Thanks also go to Marko Vuckovic from the University of Nova Gorica for the help with the Matlab software changes. The work at ETH for NB was partly funded through an Erasmus scholarship. GT was supported by the Ecosystems core research programme at the British Antarcttic Survey. The research leading to these results has received funding from the European Community's Seventh Framework Programme (FP7 2007–2013) under grant agreement no. 238366.

Edited by: W. Smith

References

Almogi-Labin, A., Hemleben, C., and Meischner, D.: Carbonate preservation and climatic changes in the central Red Sea during the last 380 kyr as recorded by pteropods, Marine Micropaleontology, 33, 87–107, doi:10.1016/S0377-8398(97)00034-0, 1998.

Acker, J. G. and Byrne, R. H.: The influence of surface state and saturation state on the dissolution kinetics of biogenic aragonite in seawater, Am. J. Sci., 289, 1098–1116, 1989.

Andersen, V., Sardou, J., and Gasser, B.: Macroplankton and micronekton in the northeast tropical Atlantic: abundance, community composition and vertical distribution in relation to different trophic environments, Deep-Sea Res. Pt. I, 44, 193–222, doi:10.1016/S0967-0637(96)00109-4, 1997.

Bednaršek, N., Tarling, G., Fielding, S., and Bakker, D.: Population dynamics and biogeochemical significance of *Limacina helicina antartica* in the Scotia Sea (Southern Ocean), Deep-Sea Res. Pt. II, 59–60, 105–116, doi:10.1016/j.dsr2.2011.08.003, 2012.

Bernard, K. S. and Froneman, P. W.: Trophodynamics of selected mesozooplankton in the west-Indian sector of the Polar Frontal Zone, Southern Ocean, Polar Biol., 28, 594–606, doi:10.1007/s00300-005-0728-3, 2005.

Bernard, K. S. and Froneman, P. W.: The sub-Antarctic euthecosome pteropod, *Limacina retroversa*: Distribution patterns and trophic role, Deep-Sea Res. Pt. I, 56, 582–598, doi:10.1016/j.dsr.2008.11.007, 2009.

Berner, R. A. and Honjo, S.: Pelagic sedimentation of aragonite: its geochemical significance, Science, 211, 940–942, 1981.

Blachowiak-Samolyk, K., Søreide, J. E., Kwasniewski, S., Sundfjord, A., Hop, H., Falk-Petersen, S., and Hegseth, E. N.: Hydrodynamic control of mesozooplankton abundance and biomass in northern Svalbard waters (79–81° N), Deep-Sea Res. Pt. II, 55, 2210–2224, 2008.

Böer, M., Gannefors, C., Kattner, G., Graeve, M., Hop, H., and Falk-Petersen, S.: The Arctic pteropod *Clione limacina*: seasonal lipid dynamics and life-strategy, Mar. Biol., 147, 707–717, 2005.

Boysen-Ennen, E., Hagen, W., Hubold, G., and Piatkowski, U.: Zooplankton biomass in the ice-covered Weddell Sea, Antarctica, Mar. Biol., 111, 227–235, 1991.

Broughton, E. A. and Lough, R. G.: A direct comparison of MOCNESS and Video Plankton Recorder zooplankton abundance estimates: Possible application for augmenting net sampling with video systems, Deep-Sea Res. Pt. II, 53, 2789–2807, doi:10.1016/j.dsr2.2006.08.013, 2006.

Buitenhuis, E. T., Vogt, M., Moriarty, R., Bednaršek, N., Doney, S. C., Leblanc, K., Le Quéré, C., Luo, Y.-W., O'Brien, C., O'Brien, T., Peloquin, J., Schiebel, R., and Swan, C.: MAREDAT: towards a World Ocean Atlas of MARine Ecosystem DATa, Earth Syst. Sci. Data Discuss., 5, 1077–1106, doi:10.5194/essdd-5-1077-2012, 2012.

Clarke, C. and Roff, J. C.: Abundance and Biomass of Herbivorous Zooplankton off Kingston, Jamaica, with Estimates of their Annual Production, Estuar. Coast. Shelf S., 31, 423–437, 1990.

Daase, M. and Eiane, K.: Mesozooplankton distribution in northern Svalbard waters in relation to hydrography, Polar Biol., 30, 969–981, doi:10.1007/s00300-007-0255-5, 2007.

Dadon, J. R. and Masello, J. F.: Mechanisms generating and maintaining the admixture of zooplanktonic molluscs (Euthecosomata: Opistobranchiata: Gastropoda) in the Subtropical Front of the South Atlantic, Mar. Biol., 135, 171–179, 1999.

Davis, C. S. and Wiebe, P. H.: Macrozooplankton Biomass in a Warm-Core Gulf Stream Ring: Time Series Changes in Size Structure, Taxonomic Composition, and Vertical Distribution, J. Geophys. Res., 90, 8871–8884, 1985.

Dietrich, G., Kalle, K., Krauss, W., and Siedler, G.: Allgemeine Meereskunde, 3, Auflage, Gebruder Borntrager, Berlin, Stuttgart, 593 pp., 1975.

Dvoretsky, V. G. and Dvoretsky, A. G.: Summer mesozooplankton distribution near Novaya Zemlya (eastern Barents Sea), Polar Biol., 32, 719–731, doi:10.1007/s00300-008-0576-z, 2009.

Elliot, T. D., Tang, K. W., and Shields, A. R.: Mesozooplankton beneath the summer sea ice in McMurdo Sound, Antarctica: abundance, species composition and DMSP content, Polar Biol., 32, 113–122, doi:10.1007/s00300-008-0511-3, 2009.

Fabry, V. J.: Aragonite production by pteropod molluscs in the subarctic Pacific, Deep-Sea Res., 36, 1735–1751, doi:10.1016/0198-0149(89)90069-1, 1989.

Fernandez de Puelles, M. L., Alemany, F., and Jansa, J.: Zooplankton time-series in the Balearic Sea (Western Mediterranean): Variability during the decade 1994–2003, Prog. Oceanogr., 74, 329–354, doi:10.1016/j.pocean.2007.04.009, 2007.

Flores, H., van Franeker, J.-A., Cisewski, B., Leach, H., van de Putte, A. P., Meesters, E. H. W. G., Bathmann, U., and Wolff, W. J.: Macrofauna under sea ice and in the open surface layer of the Lazarev Sea, Southern Ocean, Deep-Sea Res. Pt. II, 58, 1948–1961, doi:10.1016/j.dsr2.2011.01.010, 2011.

Foster, B. A.: Composition and Abundance of Zooplankton Under the Spring Sea Ice of McMurdo Sound, Antarctica, Polar Biol., 8, 41–48, 1987.

Froneman, P. W., Pakhomov, E. A., and Treasure, A.: Trophic importance of the hyperiid amphipod, *Themisto gaudichaudi*, in the Prince Edward Archipelago (Southern Ocean), Polar Biol., 23, 429–436, 2000.

Gannefors, C., Böer, M., Kattner, G., Graeve, M., Eiane, K., Gulliksen, B., Hop, H., and Falk-Petersen, S.: The Arctic sea butterfly *Limacina helicina*: lipids and life strategy, Mar. Biol., 147, 169–177, doi:10.1007/s00227-004-1544-y, 2005.

Gangstø, R., Gehlen, M., Schneider, B., Bopp, L., Aumont, O., and Joos, F.: Modeling the marine aragonite cycle: changes under rising carbon dioxide and its role in shallow water $CaCO_3$ dissolution, Biogeosciences, 5, 1057–1072, doi:10.5194/bg-5-1057-2008, 2008.

Gilmer, R. W.: In situ observations of feeding in thecosomatous pteropod molluscs, Am. Malacol. Bull., 8, 53–59, 1990.

Gilmer, R. W. and Harbison, G. R.: Diet of *Limacina helicina* (Gastropoda: Thecosomata) in Arctic waters in midsummer, Mar. Ecol.-Prog. Ser., 77, 125–134, 1991.

Glover, D. M., Jenkinds, W. J., and Doney, S. C.: Modelling Methods for Marine Science, Cambridge University Press, Cambridge, UK, ISBN 978-0-521-86783-2, 2011.

Harbison, G. R. and Gilmer, R. W.: Swimming, buoyancy and feeding in shelled pteropods: a comparison of field and laboratory observations, J. Mollus. Stud., 58, 337–339, doi:10.1093/mollus/58.3.337, 1992.

Harris, R. P., Wiebe, P. H., Lenz, J., Skjoldal, H.-R., and Huntley, M.: Zooplankton methodology manual, Elsevier Academic Press, London, UK, 684 pp., 2000.

Hopkins, T. L.: Midwater food web in McMurdo Sound, Ross Sea, Antarctica, Mar. Biol., 96, 93–106, doi:10.1007/BF00394842, 1987.

Hunt, B. P. V. and Hosie, G. H.: The seasonal succession of zooplankton in the Southern Ocean south of Australia, part I: The seasonal ice zone, Deep-Sea Res. Pt. I, 53, 1182–1202, doi:10.1016/j.dsr.2006.05.001, 2006.

Hunt, B. P. V., Pakhomov, E. A., Hosie, G. W., Siegel, V., Ward, P., and Bernard, K.: Pteropods in Southern Ocean ecosystems, Prog. Oceanogr., 78, 193–221, doi:10.1016/j.pocean.2008.06.001, 2008.

Jackson, G. A., Najjar, R. G., and Toggweiler, J. R.: Flux feeding as a mechanism for zooplankton grazing and its implications for vertical particulate flux, Limnol. Oceanogr., 38, 1328–1332, 1993.

Karnovsky, N. J., Hobson, K. A., Iverson, S., and Hunt Jr., G. L.: Seasonal changes in the diets of seabirds in the North Water Polynya: a multiple-indicator approach, Mar. Ecol.-Prog. Ser., 357, 291–299, 2008.

Koppelmann, R., Weikert, H., Halsband-Lenk, C., and Jennerjahn, T. C.: Mesozooplankton community respiration and its relation to particle flux in the oligotrophic eastern Mediterranean, Global Biogeochem. Cy., 18, GB1039, doi:10.1029/2003GB002121, 2004.

Lalli, C. M.: Structure and function of the buccal apparatus of *Clione limacina* (Phipps) with a review of feeding in gymnosomatous pteropods, J. Exp. Mar. Biol. Ass. UK, 4, 101–118, 1970.

Lalli, C. M. and Gilmer, R. W.: Pelagic snails: the biology of holoplanktonic gastropod molluscs, Stanford, Stanford University Press, California, 1989.

Larson, R. J.: Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific, J. Exp. Mar. Biol. Ecol., 99, 107–120, doi:10.1016/0022-0981(86)90231-5, 1986.

Leblanc, K., Aristegui, J., Armand, L., Assmy, P., Beker, B., Bode, A., Breton, E., Cornet, V., Gibson, J., Gosselin, M.-P., Kopczynska, E., Marshall, H., Peloquin, J., Piontkovski, S., Poulton, A. J., Queguiner, B., Schiebel, R., Shipe, R., Stefels, J., van Leeuwe, M. A., Varela, M., Widdicombe, C., and Yallop, M.: A global diatom database – abundance, biovolume and biomass in the world ocean, Earth Syst. Sci. Data Discuss., 5, 147–185, doi:10.5194/essdd-5-147-2012, 2012.

Le Quéré, C., Harrison, S. P., Prentice, C., Buitenhuis, E. T., Aumonts, O., Bopp, L., Claustre, H., da Cunha, L. C., Geider, R., Giraud, X., Klaas, C., Kohfeld, K. E., Legendre, L., Manizza, M., Plattss, T., Rivkin, R., Sathyendranath, S., Uitz, J., Watson, A. J., Wolf-Gladrow, D.: Ecosystem dynamics based on plankton functional types for global ocean biochemistry models, Glob. Change Biol., 11, 2016–2040, 2005.

Little, W. S. and Copley, N. J.: WHOI Silhouette DIGITIZER, Version 1.0, Users Guide, WHOI Technical Report, Woods Hole Oceanographic Institution, 2003.

Lochte, K. and Pfannkuche, O.: Processes driven by the small sized organisms at the water-sediment interface, in: Ocean Margin Systems, edited by: Wefer, G., Billet, D., Hebbeln, D., Jørgensen, B. B., Schlüter, M., and Weering, T. C., Springer, Heidelberg, Germany, 2003.

Longhurst, A.: Ecological Geography of the Sea, Academic Press, USA, 2007.

Luo, Y.-W., Doney, S. C., Anderson, L. A., Benavides, M., Bode, A., Bonnet, S., Bostrom, K. H., Bottjer, D., Capone, D. G., Carpenter, E. J., Chen, Y. L., Church, M. J., Dore, J. E., Falcon, L. I., Fernandez, A., Foster, R. A., Furuya, K., Gomez, F., Gundersen, K., Hynes, A. M., Karl, D. M., Kitajima, S., Langlois, R. J., LaRoche, J., Letelier, R. M., Maranon, E., McGillicuddy Jr., D. J., Moisander, P. H., Moore, C. M., Mourino-Carballido, B., Mulholland, M. R., Needoba, J. A., Orcutt, K. M., Poulton, A. J., Raimbault, P., Rees, A. P., Riemann, L., Shiozaki, T., Subramaniam, A., Tyrrell, T., Turk-Kubo, K. A., Varela, M., Villareal, T. A., Webb, E. A., White, A. E., Wu, J., and Zehr, J. P.: Database of diazotrophs in global ocean: abundances, biomass and nitrogen fixation rates, Earth Syst. Sci. Data Discuss., 5, 47–106, doi:10.5194/essdd-5-47-2012, 2012.

Marrari, M., Daly, K. L., Timonin, A., and Semenova, T.: The zooplankton of Marguerite Bay, Western Antarctic Peninsula – Part I: Abundance, distribution, and population response to variability in environmental conditions, Deep-Sea Res. Pt. II, 58, 1599–1613, doi:10.1016/j.dsr2.2010.12.007, 2011.

Mazzocchi, M. G., Christou, E., Rastaman, N., and Siokou-Frangou, I.: Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean): I. General aspects, Oceanol. Acta, 20, 521–535, 1997.

Mileikovsky, S. A.: Breeding and larval distribution of the pteropod *Clione limacina* in the North Atlantic, Subarctic and North Pacific Oceans, Mar. Biol., 6, 317–334, 1970.

Milliman, J. D. and Droxler, A. W.: Neritic and pelagic carbonate sedimentation in the marine environment: Ignorance is not bliss, Geologische Rundschau, 85, 496–504, 1996.

Moraitou-Apostolopoulou, M., Zervoudaki, S., and Kapiris, K.: Mesozooplankton abundance in waters of the Aegean Sea, Hellenic Center of Marine Research, Institut of Oceanography, Hydrodynamics and Biogeochemical Fluxes in the Straits of the Cretan Arc (project), Greece, 2008.

Mousseau, L., Fortier, L., and Legendre, L.: Annual production of fish larvae and their prey in relation to size-fractioned primary production (Scotian Shelf, NW Atlantic), ICES J. Mar. Sci., 55, 44–57, 1998.

Nishikawa, J., Matsuura, H., Castillo, L. V., Wilfredo, L. C., and Nishida, S.: Biomass, vertical distribution and community structure of mesozooplankton in the Sulu Sea and its adjacent waters, Deep-Sea Res. Pt. II, 54, 114–130, doi:10.1016/j.dsr2.2006.09.005, 2007.

NMFS-COPEPOD: The Global Plankton Database, NOAA National Oceanic and Atmospheric Administration, US Department of Commerce (http://www.st.nfms.noaa.gov/plankton), 2011.

Pakhomov, E. A. and Perissinotto, R.: Mesozooplankton community structure and grazing impact in the region of the Subtropical Convergence south of Africa, J. Plankton Res., 19, 675–691, 1997.

Pane, L., Feletti, M., Francomacaro, B., and Mariottini, G. L.: Summer coastal zooplankton biomass and copepod community structure near Italian Terra Nova Base (Terra Nova Bay, Ross Sea, Antarctica), J. Plankton Res., 26, 1479–1488, doi:10.1093/plankt/fbh135, 2004.

Perissinotto, R.: Mesozooplankton size-selectivity and grazing impact on the phytoplankton community of the Prince Edward Archipelago (Southern Ocean), Mar. Ecol.-Prog. Ser., 79, 243–258, 1992.

Ramfos, A., Isari, S., and Rastaman, N.: Mesozooplankton abundance in water of the Ionian Sea (March 2000), Department of Biology, University of Patras, 2008.

Rogachev, K. A., Carmack, E. C., and Foreman, M. G. G.: Bowhead whales feed on plankton concentrated by estuarine and tidal currents in Academy Bay, Sea of Okhotsk, Cont. Shelf Res., 28, 1811–1826, doi:10.1016/j.csr.2008.04.014, 2008.

Schalk, P. H.: Spatial and seasonal variation in pteropods (Mollusca) of Indo-Malayan waters related to watermass distribution, Mar. Biol., 105, 59–71, 1990.

Schiebel, R. and Movellan, A.: First-order estimate of the planktic foraminifer biomass in the modern ocean, Earth Syst. Sci. Data, 4, 75–89, doi:10.5194/essd-4-75-2012, 2012.

Schiebel, R., Waniek, J., Zeltner, A., and Alves, M.: Impact of the Azores Front on the distribution of planktic foraminifers, shelled gastropods, and coccolithophorids, Deep-Sea Res. Pt. II, 49, 4035–4050, 2002.

Schnack-Schiel, S. B. and Cornils, A.: Zooplankton abundance measured on Apstein net samples during cruise CISKA2005,

Alfred Wegener Institute for Polar and Marine Research, Science for the Protection of Indonesian Coastal Environment (project), Bremerhaven, 2009.

Seibel, B. A. and Dierssen, H. M.: Cascading trophic impacts of reduced biomass in the Ross Sea, Antarctica: Just the tip of the iceberg?, Biol. Bull., 205, 93–97, 2003.

Siokou-Frangou, I., Christou, E., and Rastman, N.: Mesozooplankton abundance in waters of the Ionian Sea, Hellenic Center of Marine Research, Institut of Oceanography, Physical Oceanography of the Eastern Mediterranean (project), Greece, 2008.

Solis, N. B. and von Westernhagen, H.: Vertical distribution of Euthecosomatous Pteropods in the Upper 100 m of the Hilutangan Channel, Cebu, The Philippines, Mar. Biol., 48, 79–87, 1978.

Swadling, K. M., Penot, F., Vallet, C., Rouyer, A., Gasparini, S., Mousseau, L., Smith, M., and Goffart, A.: Interannual variability of zooplankton in the Dumont d'Urville sea (139° E–146° E), east Antarctica, 2004–2008, Polar Sci., 5, 118–133, doi:10.1016/j.polar.2011.03.001, 2011.

Tréguer, P., Legendre, L., Rivkin, R. T., Raueneau, O., and Dittert, N.: Water column biogeochemistry below the euphotic zone, Ocean biogeochemistry: The role of the ocean carbon cycle in global change, edited by: Fasham, M. J. R., Global Change – The IGBP Series (closed), 145–156, doi:10.1007/978-3-642-55844-3_7, 2003.

Van der Spoel, S.: Growth, reproduction and vertical migration in *Clio pyramidata* Linne, 1767 forma *lunceolata* (Lesueur, 1813), with notes on some other Cavoliniidae (Mollusca, Pteropoda), Beaufortia, 281, 117–134, 1973.

Volkov, A. F.: Mean Annual Characteristics of Zooplankton in the Sea of Okhotsk, Bering Sea and Northwestern Pacific (Annual and Seasonal Biomass Values and Predominance, ISSN 1063-0740, Russ. J. Mar. Biol., 34, 437–415, doi:10.1134/S106307400807002X, 2008.

Ward, P., Whitehouse, M., Shreeve, R., Thorpe, S., Atkinson, A., Korb, R., Pond, D., and Young, E.: Plankton community structure south and west of South Georgia (Southern Ocean): Links with production and physical forcing, Deep-Sea Res. Pt. I, 54, 1871–1889, doi:10.1016/j.dsr.2007.08.008, 2007.

Wells Jr., F. E.: Effects of Mesh Size on Estimation of Population Densities of Tropical Euthecosomateus Pteropods, Mar. Biol., 20, 347–350, 1973.

Wells Jr., F. E.: Seasonal patterns of abundance and reproduction of euthecosomatous pteropods off Barbados, West Indies, Veliger, 18, 241–248, 1976.

Werner, I.: Living conditions, abundance and biomass of under-ice fauna in the Storfjord area (Western Barents Sea, Arctic) in late winter (March 2003), Polar Biol., 28, 311–318, 2005.

Wormuth, J. H.: Vertical distributions and diel migrations of Euthecosomata in the northwest Sargasso Sea, Deep-Sea Res., 28, 1493–1515, doi:10.1016/0198-0149(81)90094-7, 1981.

Wormuth, J. H.: The role of cold-core Gulf Stream rings in the temporal and spatial patterns of euthecosomatous pteropods, Deep-Sea Res., 32, 773–788, 1985.

Zervoudaki, S., Christou, E., Siokou-Frangou, I., and Zoulias, T.: Mesozooplankton abundance in water of the Aegean Sea, Hellenic Center of Marine Research, Institut of Oceanography, Invest. of new marine biol. resources in deep waters of Ionian and Aegean Seas, Greece, 2008.

ZooDB – Zooplankton database, Plankton sample analysis supported by NSF grants to M. D. Ohman, Scripps Institution of Oceanography and by the SIO Pelagic Invertebrates Collection, http://oceaninformatics.ucsd.edu/zoodb/#, 2011.