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LETTER

Relative exposure to microplastics and prey for a pelagic forage fish

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Abstract

In the global ocean, more than 380 species are known to ingest microplastics (plastic particles less than 5 mm in size), including mid-trophic forage fishes central to pelagic food webs. Trophic pathways that bioaccumulate microplastics in marine food webs remain unclear. We assess the potential for the trophic transfer of microplastics through forage fishes, which are prey for diverse predators including commercial and protected species. Here, we quantify Northern Anchovy (*Engraulis mordax*) exposure to microplastics relative to their natural zooplankton prey, across their vertical habitat. Microplastic and zooplankton samples were collected from the California Current Ecosystem in 2006 and 2007. We estimated the abundance of microplastics beyond the sampled size range but within anchovy feeding size ranges using global microplastic size distributions. Depth-integrated microplastics (0–30 m depth) were estimated using a depth decay model, accounting for the effects of wind-driven vertical mixing on buoyant microplastics. In this coastal upwelling biome, the median relative exposure for an anchovy that consumed prey 0.287–5 mm in size was 1 microplastic particle for every 3399 zooplankton individuals.
Microplastic exposure varied, peaking within offshore habitats, during the winter, and during the day. Maximum exposure to microplastic particles relative to zooplankton prey was higher for juvenile (1:23) than adult (1:33) anchovy due to growth-associated differences in anchovy feeding. Overall, microplastic particles constituted fewer than 5% of prey-sized items available to anchovy. Microplastic exposure is likely to increase for forage fishes in the global ocean alongside declines in primary productivity, and with increased water column stratification and microplastic pollution.

1. Introduction

Microplastic particles (<5 mm in size) enter marine food webs when animals directly and indirectly consume them [1, 2]. Direct consumption occurs when an organism ingests microplastic from the environment; indirect consumption occurs when an organism ingests prey containing microplastic. Currently, more than 380 marine species are known to consume microplastics including mammals [3], zooplankton [4], mollusks [5, 6], sea turtles [7], and fishes [8]. Direct and indirect microplastic consumption may exert a range of impacts on organism physiology and fitness, such as disruption to feeding, reproduction, and immunity [9, 10]. The extent of physiological and ecological consequences of microplastic consumption is not well known. More so, the relative contributions of direct and indirect microplastic consumption to the broader cycling of microplastics within marine food webs remain unknown.

Juvenile and adult Northern Anchovy (*Engraulis mordax*, 1–4 years old) feed on prey in the same size range (0.287- 5 mm) as microplastic particles [11, 12). *A:;* anchovy grow the morphology of their feeding apparatus changes and limits their consumptionof smaller particles and prey (12). Filtre-feeding forage fishes such as anchovy may be particularly suscepn'ble to high levels of microplastic ingestion because they can filter multiple liters of water per minute (13, 14). Microplastic consumption by anchovy has been examined with laborato.ry stud - ies and fish gut content analy-.es (15- 21). However, none haveexamined the initialexposureof anchovies to microplastics relative to their natural zooplankton prey across their vertical habitat. More than 490 marine species feed on juvenile and adult forage fishes (including anchovies), such as seabirds (pelicans), marine mammals {sea lions), and commercialfishspecies (tuna) (22-25). Giventhe wi<le range of predators that feed on anchovy, they ar,e thus a likely trophic pathway for the cycling of microplastic particleswithin marinefoodwebs.

We assess the relative exposure of Northern Anchovyto microplastics compared to their primary zooplankton prey, which we refer to as anchovy microplasticexposurein thispaper. Our studyinvestigates anchovy microplastic exposure in the southern California Current Ecosystem (CCE). The CCE is a produ ctive eastern boundary upwelling system that supports commercial fisheries, marine mammals, and protectedspeciessuchasseabirds [26) . We ana1yu hydrographic, microplastic, and zooplankton dataconcurrently collectedacrossfom seasons in 2006 and 2007. Specifically, we quantify: (1) the relativeexposure of Northern Anchovy to microplastics compared to their naturalpreyin the southern CCE; (2) spatial and temporalshiftsin relativemicroplastic exposure; and (3) the role of anchovy body, size on relative microplastic exposure. Our study provides a preliminary assessment of how, and to **what** degree, microplastics enter marine food webs through midtrophiclevelspecies.

2.Methods

Northern Anchovy *(Engraulis mordax)* are present throughout the mixed layer (-0-20 m depth) in the CCE (figure 1 (a)) [27]. To quantify Northern Anchovy microplastic exposure in the CCE,. we first performedaliteraturesearch to identifyconcurrently collected microplastic and zooplankton ab:undance data. Wesearchedforarticleswiththe keywords'California' AND 'microplastic' AND 'zooplank-ton' in Webof Science. Our reviewproduceda singleapplicablestudy, region-the southern CCE. We incorporated historical data from the southern CCE collected through the California Cooperative Oce-anic Fisheries Investigations {CalCOPI) and California Current Ecosystem Long Term Ecological Research programs (figure 1 (a)). Microplastic and zooplanl-ton samples were taken on lines 80 and 90 of the CalCOPI sampling grid duringfour research cruises from 2006 (April, July, October) and 2007 {January) {figures 1 (b) and {c)).

2.1. Anchovypreysittestimation

Anchovygillrakerspacinglimits the sizeof th e smallest microplastic particle and prey an anchovy can consume [12). To quantify shifts in anchovy exposure to microplastics and zooplankton within the relevant size ranges for anchovies of different ages, we used a historical dataset that documented increases in gillraker spacing with anchovy growth (12). We estimated exposure for juvenile to adult anchovy, -1-4yearsold, ranging in size from 7 150 mmin standard length (29). Juvenile to adult anchovy had corresponding incre-ases in gill raker spacing from 0.287 to 0.493 mm {figure 2(a)). Both juveniles and adults preferentially feed on larger mesozooplankton (30) and derive a significant port ion of their energy from zooplanl-ton up to 5 mm in size [11). Thus, we set the upper size *limit* of anchovy prey items to be 5 mm to correspond with the maximum established microplastic particle size range {figure 2(b)).

2.2. Surface microplastic collection and abundance estimates

Doyle *et al* (2011) provides a detailed description of howplasticparticleswerecollectedatsea (31). Briefly, plastics from 0.714-15 mm in size were collected usinga 505-μ m mesh manta net towedat the surface for approximately 15 min at - J.5- 2 knots (n = 79 tows, figure 1{a)). We assumed that most microplasticparticles are non-spherical with the potential to pass through the net dependenton particleorientation. Thus, only microplastics larger than or equal to the diagonal of the mesh opening {> 0.714 mm) were likely reliably collected. The longest dimension of each microplastic particle was recorded by an independent laboratory as detailed in Doyle *et al* {2011) (31).

We applied the correction factor (*CF)* from Koelmans *et al* (2020) to the sampled plastic size range to estimate microplasticabundancewithin the feeding size range of anchovy (32) figure{2{b)). The sampled{or measured) plastic size minimum {x!M) and maximum ("'2.M) was 0.714 and 15 mm, respectively. The default (or estimated) plastic size minimum{x₁o) and maximum (xw) within the feeding sizerangeof anchovy was 0.287 and 5 mm, respectively.The default plasticsizeminimumchanged with anchovy growth, increasing from 0.287to 0.493 mm for juvenile to adult anchovy. A fitting parameter, a = 1.6, was included and based on **14** size distn'butions of microplastics (32, 33). The full equation is detailed below:

$$CF= (xk'' - xlo'') (4 \quad t - xht) \quad 1$$

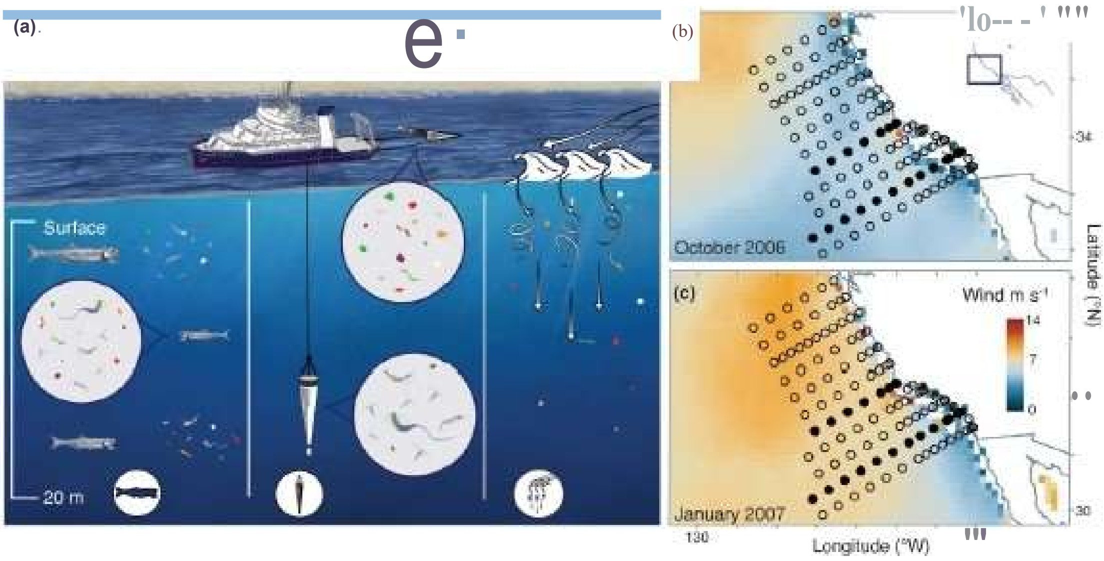

Figure 1. Mdhods andsamplingregion.(a) Sowcc• and modelingtcclutiquea W>Cdto quantifymicroplasticandzooplankton abunda.J1ce• in theCaliforniaCurrentEcoayatem. Left: NorthernAnchovy (*Engraulisrnordmc*) lugdyfor:agcfromO to 20 m depth, wheretheyc.ncountcr microplasticaand their zoopla..nkton prey. *U:rd.tr.In situ* piingofsurf.acemicroplartiu w.inga manta net (top) anddepth- integratedsampling of rooplankton winga PRPOOS (Planktonic RateProcessc• in Oligotrophk Ocean System•) net (bottom). *Right:* Model crtimation of po aitivcty buoyant plastics no t sampled due to vcrticalm.ixi.ng from wind mesa.((b) and (c)) CalCOPl (CaliforniaCoopc:ratn<:cOceanicPiahetic•lD:,-.crtigation) samplinggrido on monthlymem windspeed(m-. [1]) at 10 m abc„-".<thesea surf.ace. Smitccoticroplasticsanddepth-integrated zooplaakton pleaw""ac collectedandenumerated at all6lkdinatatioru(n = 20 nationspercruise). Wind6})«ddataa.-re &om theCross-Cfflbrated Multi-Platform O=.nSurface Wmd Allaly,«fi>r(b) October 2006(c) and January 200 7 (28). lliuatratio.. in (a) byKLance.

2.3. Depth-integrated (0-30m depth) microplastic abwtdance estimates

Wmdspeeds greater than 4 ms ı at 10 m a bo ve t he ,ie-a surface (U_{10} > 4 ms [1]) drive ne-ar-surface verticalmixingthattransportspositivelybuo}'llllt microplasticsbeneaththeseasurfuce (34). Weuseda simple model to estimate the total abundance of positively buoyant microplastics, N (# m •), including those not sampled due to wind-driven mixing and the downward transport of microplastics (figure 1{a)) (34). SeetableAl for a fulldescriptionof modelparameters and values. The depth decay model accounted for the abundance of microplastics collected in the net, N,.,. (# m •), the immersion depth of the net, d {m), the microplastic rise speed, wi, (m s ı), and near-surface mixing due to bre-aking waves, A,, {m2 • ') :

$$N = N_{t.w}\{1 - \exp\{-m \qquad . ^{1}))\ \mathrm{I}$$

The rise speed of plastic, wi, , was not directly measured. Based on our particle sizerange, we selectedariserateof0.009ms ı whichcorresponded with measured rise speeds of microplastics ranging from, 0.5-1 mmin size (35).

Following Kukulka *et al* {2012) (34), the degree of near-surface mixing, A_0 (m^2 s ı), was estimated based on the drag coefficien,t C;, air density, p. (kgm •), thewindspeed lOmaboveseasurface, U_{10} {m s ı), water density, p .,., (kgm •), thevonKarman constant, K-, gravity, g (m s [2]), and wave age, a:

$$A_{,,} = 1.5 \left(\frac{C\ p\ [P.}{d\ p_{,..,,,}} \right) \ \mathrm{IO}\ \ 1<0.96g \ \ ^{\mathrm{I}}afC;1u10$$

Parameter values used to estimate A_0 were taken from best available data. For April, July, and October2006, weusedunderway shipdatarecordedat the time of the net tows. Underway ship data were not available for January 2007- we instead used hydrographic data recorded during a CTD cast on this **same cruise at the same stations where the net tows** occurred. Seawater density for all cruises was taken fromhydrographicdata collected at the samestations as the net tOWll. The *r,,lnlp* function from the se-a-**mat package in MATLAB wasused to convert recor**ded air temperature and relative humidity into air density{for cruises in 2006) and recorded dry and wet temperature into relative humidity and then air density (forJanuary 2.007), For all cruis the *cdnlp* function from the sea-mat package in MATLAB was used to convert recorded wind speedand ship anemometer height into wind speed 10 m above the ,ie-a surface (U_{10}) and the dragcoefficient (C,). A com**ponent of near-surface mixing, waveage,<ı, was not** readily available To estimate waveage, we usedavailable underwayship datatoinvestigatewindspeedand wind direction pre- and post-net tOWll. Wmds were primarily unidirectional and steady surrounding the collection (figure A1). As such, we chosea waveage of 35 to correspond with a fully developed se-a (34). The instantaneous wind speeds during net tow.: are available in figure A2.

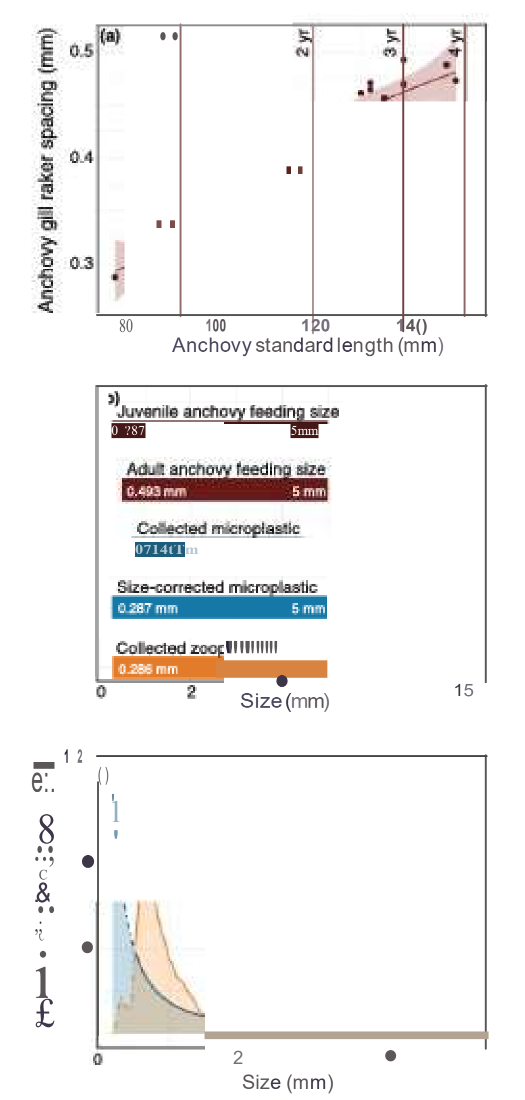

Figure 2. The ran-gein Northern Anchovy preyme ill relation to the size of sampled mkroplamcs and z.ooplaakton. (a) Change in meaninte-rakergill ,pacingfor juvenileandadul l anchovy with6ahbody growth (n= 29). \bticallines represent the approximate ageofanchovy in year Increue in gill raker6P3cingwithincre3ainganchovyst.and.udleng.th uk.,n&omR)>ka=---.ki (2009) (12). Length-age relationship of northernanchovy take.afrom Baxter (1967), originally &omCwk and Phillip,(1952) (29). Curve andshadingrepresent a LOESSfit witha 95%, confiden-cei.ntc:rnl. (b) 'Iheran-geinanchovypreyriu shifts&om0.287- 5 mmto0.493-5 mm for jUt\c.nik lto adultanchovydue to da.ifu:in gillrakerspacingwith anchovygrowth. Micropluti.ca &om0.714 to 15 aun in aiu werecollected. Raw microplastic abundance• \\"tte aiu -oorrcctcdbal.led offKoclmaru6t o1 (2020) to emlll.ate theabundance of m.icroplu tics with.inanchovy feedingai-u rangc-• (0.2 87 - S mm) ('2). Zoopb:nkton &om0.286 to 5 mm inai-u wc:-re colkctcd. (c) 'Ihe proportional abundance of depth-integrated. aiu -oorrcctd microplartica (blue) and zooplankton (orange) in relrtion to theirme . Proportional abundance basiedon the m<di:an total bundanccof nticroplarticpartidcs androoplankton individuals acros allnations andsamplingperiods. Linctype representsthesi-zerangeofpreythatallmedas-.siesof anchovy foedon (-) '\'CnUS thesizerange of prey that onlysm.alkranchovycanconsistentlyfeedon (·-)M

The estimated maximum depth of microplastic particletransport was based on the same windmixing model from Kukulka *et al* {2012) (34); between thesurface andthismaximum depthiswhere99% of microplasitc particles were present (34). The abundance of microplastic particles at a given depth, $n(z)$ {ii m ' }, is a function of the microplastic particle abundance at the swface, n_0 (ii m ^{3}), the depth, z {m), plastic risespeed, w_i, (m s ^{1}), and ne-ar-surface mixing, $A_{,}$, {m^2 S I):

$$n(z) \quad n.exp(2WJ,A^{1})$$

2.4. Zooplankton collection and abtwdance estimates

Zooplankton individuals with a longest dimension between 0.286 and 5 mm in size were collected usinga 202-µm Planktonic Rate Processes in Oligotrophic Ocean Systems (PRPOOS} net (figuresl(a) and 2(b)). The PRPOOS net was towed vertically, ascending from -210 mto thesurface at a rate of 50 m per minute, during the day (n = 44 tows) and night (n = 35 tow.:) (figure A3}. We again **assumed moot zooplankton are non-spherical, and** thus that only zooplankton larger than or equal to the diagonal of the mesh opening were consistently collected (> 0.286 mm). See Gonky *et al* (2010) for a full description of zooplankton quantification and measuring methods [36]. Briefly, all individuals from a representativealiquotof zooplanl-ton from each PRPOOS sample were digitally measured and enumerated using ZooScan imaging. The maximum dimensionofeach zooplankton individual wasme-asured. We assumed that zooplankton were uniformly distributed throughout the vertical sampling region when estimating zooplankton abundance (ii m '). Theprimaryconstrainton anchovy preyselectivityis preysize,nottaxonomy(37).Therefore, weassumed all zooplankton with the longest dimension within thefeedingsizerangeofanchovy (0.287- 5 mm) were available for foraging (figure 2(b)).

2.5. Calculation of anchovy relative exposure

We assumed that microplasitc particles and zooplankton prey had an equal likelihood of being consumed by anchovies. The relative microplastic **exposure ratio of an anchovy, ER, was based on** the abundance of microplastics, M (ii m ^{3}, and the abundance of their natural zooplankton prey, Z {ii m ^{3}) at eachstation- ERwascalculated as follow.::

$$ER = \frac{M}{Z}$$

2.6. Statistical analyses

We tested for significant temporal and spatial differencesin (1) microplastic abundance, (2) zooplanl'ton abundance and, {3} anchovy relative exposure to **microplastics. Non-parametric tests were usedasour** data were not normally distn'buted. The Spearman Rankcorrelationtest,Kruskal-Wallistest, and Mann-**Whitney U test were used to examine differences** in abundances and the relative microplastic exposure with distancefrom shore, sampling month, and time of day, respectively. To visualize differences in microplastic particle and zooplanl'ton abundances with distance from shore, we used a LOBSS fit with 95% confidence intervals. Median abundance and **exposw-e values for near-..hore and offs hore environ**-ments were calculated based on the median sampling distance from shore, 200 km. There were $n = 40$ nearshore stations { 200 km) and $n = 39$ offshore stations(> 200km). The proportional abundances of differentsizeclassesof zooplankton and microplastics were balledon the medianabundance of microplastic particles and :rooplanl't on individuals across all stations and sampling periods. All statistical analyses were done usingR venion 1.4.1106 (38).

3. Resul ts and discussion

Microplasticand zooplankton samples were collected from the southern CCBin 2006 and 2007 acrossfour se-asons {figure 1{a)) . There were changes in wind speed and near-surface mixing across and within s-ampling periods in the CCB{figures l (b} and {c)). The abundance of microplastics and zooplankton available to foraging anchovy differed with particle **and prey size as well as sampling location, result**-ing in differences in anchovy microplastic exposure (figures 2(a)- (c)). Anchovy microplastic exposure varied with distance from shore, time of day, s-ampling mont h, and fishbodysize. The median relative e:,:posure was l microplastic particle for every 3399 zooplankton individuals. Across all sampling periods and anchovy sizes, microplastic particles constituted fewer than 5% of the prey-sized items that anchovy potentially encountered. The rate and prevalence of microplastic particle consumption by anchovie is likely related to factors such as anchovy feeding selectivity. The relatively low exposure to microplastics we findsuggests that anchovy did not represent a significant trophic pathway fo6 microplastics into marine food webs in the CCB during the 2006 and 2007 surveys. Our results corroborate recent findings of low trophic transfer fromforage fishes to their predators (39-41). Our analysis was limited to historical data due to constraints in co-collected microplastic, zooplankton, and environmental data, however future studies may benefit from assessing recent anchovy microplastic exposure. Further research is required to comprehensively understand the impact of microplastic cons111D1pt ion by mid-trophic level species such as anchovy within marine food webs

3.1. JMicroplastic abundancein the southern CCE

Juvenile(- 1 year old) anchovy can consume microplastic particles as small as 0.287 mm in size [12), whichissmallerthan thesizerangeof plastic particles that were enumerated in CCB surveys (figures 2(a) and (b)). For this re-ason, we applied a size correction to estimate microplastic particles that occur within both the feeding size range of anchovy and the collection size range of their :rooplankton prey {0.287- 5 mm). The median surface size-corrected microplastic particle abundance was 0.198 microplastic particles m• acrossallstations and sampling periods (table 1). The surface size-corrected microplastic particle abundances are within an order of magnitude of other studies in the CCB and North Pacific Subtropical Gyre {NPSG} (42-46). **No significant differences in surface size-corrected** microplastic abundances were found with distance from shore (Spe-annan's rank correlation, $p > 0.05$) or day-night (Mann Whitney U test, $p > 0.05$) across all cruises (table 1). However, surface size-corrected microplastic abundances did vary significantly by month (Kruskal- Wallistest, $p < 0.05$; figures 3(a)-(d)). Surfacesize-corrected microplastic abundances were highest in January 2007 and lowest in October 2006, with mediansof 0.507 and 0.078 particles m •, respectively(table 1, figures3(c) and (d)).

Wmd-stressgenerates near-surface vertical mix-ing in the ocean and transports positively buoyant microplastic particles below the surface (47). Near-surface mixing during the sampling period likely prevented the collection of some positively buoyant plastics by surface net tows. Accordin gly, we applied a windcorrectionto estimatethe totaldepth-integrated abundance of positively buoyant microplastic particles. The median size-corrected microplastic abundance increased from 0.198 to 0.466 particlesm• between surface and depth -integrated **estimates across all stations and sampling periods,** signifying the importance of microplastic particles mixed deeper intothewater column {table l}. These depth-integrated microplastic abundances corroborate other regional studies investigating subsurface microplastic abundances (45, 48, 49). The extent that depth-integrated estimates of microplastic particle abundances differed from sur- face estimates varied by month (figures 3(a)- (d)). For January 2007, depth -integrated, size-corrected microplastic particle abundances were as high as an order of magnitude greater than surface, size-corrected measurements (figure 3(d)). This difference is due to increased winds speeds offahore in January 2007.

A maximum windspeed of 14 ms ı in Jan u ary 2007 resulted in an estimated transport of microplasticsdown to 30 m depth. Duringthesehighwind

Table 1. Microplastic and zooplankton abundances, and anchovy relative microplastic exposure. Statistical significance and median values for (1) the abundance of size-corrected microplastic particles and zooplankton individuals, sizes 0.287–5 mm, and (2) the ratio of microplastic particles to zooplankton individuals. Size-corrected and depth-integrated microplastic abundance estimates were based on Koelmans *et al* (2020) [32] and Kukulka *et al* (2012) [34], respectively. Samples were designated as 'nearshore' or 'offshore' based on the median sampling distance to shore (200 km), resulting in n = 40 nearshore samples (200 km) and n = 39 offshore samples (>200 km).

	Surface microplastic (# m 3)	Depth-integrated microplastic (# m 3)	Depth-integrated zooplankton (# m 3)	Microplastic abundance: zooplankton abundance
Location				
Nearshore	0.224	0.369	1918	1:4973
Offshore	0.164	0.565	536	1:714
Statistical test	Spearman's Rank correlation			
Statistical results	= 0 1823693	= 0 1152287	= 0 8016336	= 0 4997017
	p = 0.1077	p = 0.3119	p =< 2 2 10 16	p = 2 753 10 6
Month				
April-06	0.269	0.492	1590	1:3399
Jul-06	0.114	0.459	1165	1:3951
Oct-06	0.078	0.104	607	1:5941
Jan-07	0.507	3.273	1066	1:407
Statistical test	Kruskal–Wallis			
Statistical results	2 = 43.947	2 = 37.746	2 = 4.5861	2 = 19.771
	p = 1 549 10 9	p = 3 199 10 8	p = 0.2047	p = 1 893 10 4
Time of day				
Day	0.162	0.493	824	1:3667
Night	0.254	0.462	932	1:3103
Statistical test	Mann–Whitney U test			
Statistical results	W = 637	W = 787	W = 714	W = 767
	p = 0.1909	p = 0.8706	p = 0.5858	p = 0.9803
All samples (n = 79)				
	0.198	**0.466**	**914**	**1:3399**

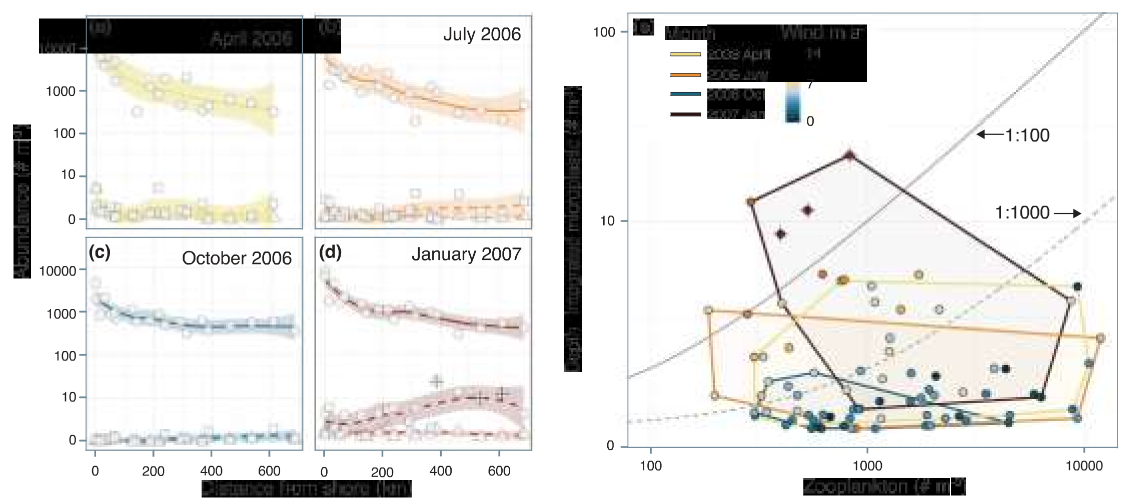

Figure 3. Relative exposure of anchovy to microplastics and their natural zooplankton prey. (a)–(d) Abundances of zooplankton ( ), depth-integrated microplastics ( ), and surface microplastics ( ), sizes 0.287–5 mm, from collections in (a) April 2006 (n = 19), (b) July 2006 (n = 20), (c) October 2006 (n = 20), and (d) January 2007 (n = 20). Curves and shading represent a LOESS fit with 95% confidence intervals. For cases where wind speeds were relatively weak, the depth-integrated and surface microplastic abundances were similar, and the curves overlap. Distance offshore estimated from the CalCOFI stations to the closest point of land. (e) Zooplankton abundances and wind-corrected (depth-integrated) microplastic abundances (sizes 0.287–5 mm) across all stations and years (n = 79). Point colors represent *in situ* wind speed (m s 1) at 10 m above the sea surface during microplastic collections. Polygons represent convex hulls for April 2006 (yellow), July 2006 (orange), October 2006 (blue) and January 2007 (red). Curves represent the ratio of microplastic particles to zooplankton individuals, 1:100 (top) and 1:1000 (bottom). Plastic size correction factors were taken from Koelmans *et al* (2020) [32]. Wind-corrected, depth-integrated microplastic abundances represent model estimates from Kukulka *et al* (2012) [34]. Model estimates of microplastic abundances may be inaccurate during high wind conditions (wind speed at 10 m above the sea surface >12 m s 1). Data collected during these high wind periods are marked with a ' + ' in panels (d) and (e).

periods, the model estimated the depth-integrated microplasitc abundanoe to be 40 times gre-ater than the surfaoe micropla,tic abundanoe. The wind mixing model may be unreliable when wind speed exceeds 12 m s ı as i t may incorrectly predict the transport ofpositivelybuoyant microplastics beneath the mixed layer. Higher microplastic densities are a,oociated with ,urfaoe collections during calm, low-wind conditions (34). Therefore, although the true depth-integratedmicropla,tic abundanoeo may not have been more than 40-fold higher than ,urfuoe abundan oeo, it is still likely that the majority of microplaotics in areas of high wind were not collected. Depth-integratedmicropla,tic abundances in regions where winds speeds were from 4 to 12 m s ı were approximately five times greater than measured ourfuce values. Wllld speeds were lower than 4 m s ı at a third of our stations {figure A2). Por these locations, we aooumed negligiole ,urfaoe mixing and that all positively buoyant microplastics wereconcentratedat the stuface. Some evidenoeexists thatwindmixingmodelo unde restimatethe abundance of oubourfuoe microplaot ics in low windcondition, (35).

The wind correction used to estimate depth-integrated microplastic particles is a simple model based on a suite of assumptions Our approach does not aocount for physical and/or biologicalm echanisms that transport neutrally and negatively buoyant plastics throughout the water column [50). In the CCB, micropla,tics are generally more abundant at the sea surfaoe [31, 45, 48). Smaller microplasticparticles(0.100-5 mm in size)aremostabundant below the mixed layer, pe-aking in abundance at 200 m depth withinthe oentralCCB[51). As anchovy primarily forage from ---0-20 m depth [27), we did not consider micropla,tics deeper than 30 m in our analysis. We assumed that ne-ar-, urfuoe mixing was the primarydriver of the vertical transport of microplastic particles, which disregards the poten tial role of seawater density differenoeo. Finally, micro plastic rise velocity determines the rate at which a vertically mixed, positively buoyant microplastic particle will return to thesurfuce. The rise velocity of microplasticparticlesdecrease,withdecreasingparticle,ize [35, 47]. In the abseJloe of available direct measurements of microplaotics abundanoe in the smallest ,ize ciaos (0.287--0.5 mm) and their associated rise velocities, there may be errors in our e.stimated particle abundan,oe

Ooean circulation inlluenoes microplastic distributions and likely inlluenoed microplastic particle abundanoes within our sampling region [50, 52). There were no visible trends from ne.a.rshore to off - shore for depth-integrated, size-corrected microplastic particleabundanoeo withinthe April, July, and October 2006 sampling periods (figures 3(a}-{c)). However, microplastic abundances did increase ,lightly with distance from shore during January 2007 (figure 3(d)). This increase could be associated with plastic entrainment into the subtropical gyre, as observed in previous studies [45, 53). Acroo, our study region, depth-integrated, size-corrected microplastic abundances ranged from O to 23 microplaotic particles per m• . Small-scale variations in microplastic abundanoes may be due to patchiness causedby physical drivers ouch as plastic laden runoff following a storm or the development of surface ,licks [44,54). Depth-integrated microplastic abundances significantly varied by month {Kruskal-Wallis test, $p < 0.05$) and were highestin January and lowest in October, aligning with surfuce micropla,tic abundanoes (table 1, figures 3(c) and (d)).

3.2. Depth-integrated zooplanktonabundance in *the* southern CCB

Depth-integrated :rooplankton abundanoes varied aocording to distance from shore, sampling period, and time of day, with a median of 914 zooplankton individuals per m• acroo, all station, and sampling periods (table 1). Zooplankton abundanoes significantly varied with distanoe from shore (Spearman's rankcorrelation, $p < 0.05$), decre-asingfromnearohore to offshore waters within our sampling grid (table 1, figures J(a}-(d)). In the CCB, coastal winds drive upwelling of nutrient-rich waters from bene-ath the mixed layer to the surface, boosting primary production and affecting zooplankton abundanoe, [55). As the effects of coastal upwellingdecrease with distanoefrom shore, increasedabundanoesofzooplankton are expected, particularly in larger zooplankton, within ne-arshore waters [56). In the region and during the time of this study, greater abundances of zooplankton and a greater relative abundanoe of larger individual, (equivalent circular diameter > 3.8mm} werereported in neap..hore waters [57). We were unable to account for small-scale changes in the spatial distribution of zooplanl-ton. Topographic features in the CCB (e.g. seamounto, canyons, and shelf breaks) may aggregate zooplanl-to,ncreating zooplankton 'hotspots' and increasing zooplankton availabilitytoanchovy[58-{)l j. Upwellingin theCCB is ottongeot from Marchto August [62]. This peakin upwelling corresponded with the highest zooplankton abundances in April and July of 2006 (table 1, figures 3(a} and (b)). Similarly, upwelling is limited during the fall, corresponding with the lowest zooplankton abundances reported in October 2006 {figure 3(c)). It should be noted that the differences in zooplankton abundance across sampling months were not significantly different (Kruskal-Wallis, $p > 0.05$; table 1). Finally, zooplankton undergo die! vertical migrations, desoending hundreds of meters below the foraging habitat of anchovies during the day (27, 63). Zooplankton werecollected during the day (n = 44 tows) and night (n = 35 tows) allowing us to investigate diel differences in zooplankton abundance (figure A3). Day and night median zooplankton abundances were 824 and 932 individuals per m^3, respectively. Although these day-night differences were not significant during the time of our surveys (table 1, Mann–Whitney, $p > 0.05$), the diurnal vertical shift in the distribution of zooplankton prey may still decrease anchovy prey availability during the day. Overall, anchovy prey were most abundant nearshore, during the spring, and at night.

3.3. Relative exposure of northern anchovy to microplastic particles vs. zooplankton prey in the southern CCE

The median relative exposure for anchovies across their vertical habitat, and within their feeding size range (0.287–5 mm), was 1 microplastic particle for every 3399 zooplankton (table 1). Across all stations and years, zooplankton were more than an order of magnitude more abundant than microplastics (figure 3(e)).

Anchovy microplastic exposure varied with distance from shore, sampling period, and time of day. Ocean circulation and productivity patterns in the CCE should result in higher relative microplastics exposure offshore and with closer proximity to the NPSG. Nearshore-offshore differences in microplastic exposure were significant (Spearman's rank correlation, $p < 0.05$), increasing by an order of magnitude from nearshore to offshore (table 1). The reported median offshore exposure (1 microplastic particle: 714 zooplankton individuals) is approximately three orders of magnitude greater than exposure reports for planktivorous fishes near the central NPSG [43]. Our work differs from previous research by estimating the abundance of positively buoyant microplastics not captured by surface collections due to near-surface mixing. Thus, it is reasonable for us to report higher microplastic exposure across the vertical habitat of a planktivorous fish compared to studies that focus their analyses on the surface. We expect anchovy microplastic exposure to continue increasing with increased proximity to the central NPSG, but our available microplastic sampling data did not cover this full spatial gradient. Adult anchovies are primarily found nearshore in the CCE, and were likely not subject to increased microplastic exposure in offshore waters [64]. Across our sampling period, the lowest and highest median microplastic exposure occurred in October 2006 and January 2007, respectively, aligning with the overall lowest and highest microplastic abundances (figures 3(c) and (d)). Finally, anchovy microplastic exposure was higher during the day than at night (table 1), likely due to daily zooplankton migration patterns. Taken together, anchovy had the highest relative microplastic exposure in offshore waters, during the winter, and during the day.

3.4. Implications of anchovy morphology and behavior on their relative exposure

Anchovy morphology and behavior affect microplastic exposure regardless of microplastic and zooplankton prey abundances. Globally, microplastic particles increase in abundance with decreasing size [32]. Therefore, the smaller the microplastic particle a fish can consume, the higher their likelihood for increased microplastic exposure. The gill rakers of juvenile anchovy, 1 year old, retain microplastic particles down to 0.287 mm in size. Conversely, adult anchovy, 4 years old, have wider gill raker spacing, preventing the consistent retention of microplastic particles smaller than 0.493 mm [12, 29] (figures 2(a) and (b)). The maximum exposure for juvenile to adult anchovy decreased from 1 microplastic particle: 23 zooplankton individuals to 1:33. Mahara *et al* (2022) [65] found that juvenile herring, a similarly zooplanktivorous species, had higher microplastic exposure than zooplankton and larval herring. This finding was similarly a product juvenile herring prey size and the size distribution of available particles and prey [65]. In the case of anchovy, feeding on large prey is more energetically favorable. Therefore, anchovy of any size may be less likely to seek out and ingest the smaller more abundant microplastic particles [30, 37, 66]. Anchovy typically filter feed during the day and particulate feed at night [66]. The less targeted feeding strategy of anchovies during the day would likely increase their relative microplastic exposure [13]. Overall, the highest microplastic exposure across all locations and sampling periods likely occurred for small, juvenile anchovy foraging during the day.

We could not account for anchovy food preferences or avoidance behavior when considering the potential relative microplastic exposure of anchovies. However, even if anchovy preferentially consumed all microplastic particles available, at a maximum, they would ingest one microplastic particle for every 20+ zooplankton individuals as microplastic particles constituted fewer than 5% of the available prey-sized items. The core habitat of Northern Anchovy is within the southern CCE, where our study was focused [67]. However, future investigations may expand into microplastic exposure throughout the wider habitat of Northern Anchovy across the central and northern CCE.

The potential physiological and ecological impacts of microplastic consumption on anchovy physiology and behavior are not well known. Ingested microplastic particles may cause intestinal damage, be retained indefinitely in the stomach, translocate to vital organs, or transfer chemical additives to fish [15, 68, 69]. Alternatively, microplastic particles may be eliminated or regurgitated by anchovies with minimal organismal impacts since microplastics are estimated to be retained in anchovy guts for approximately one

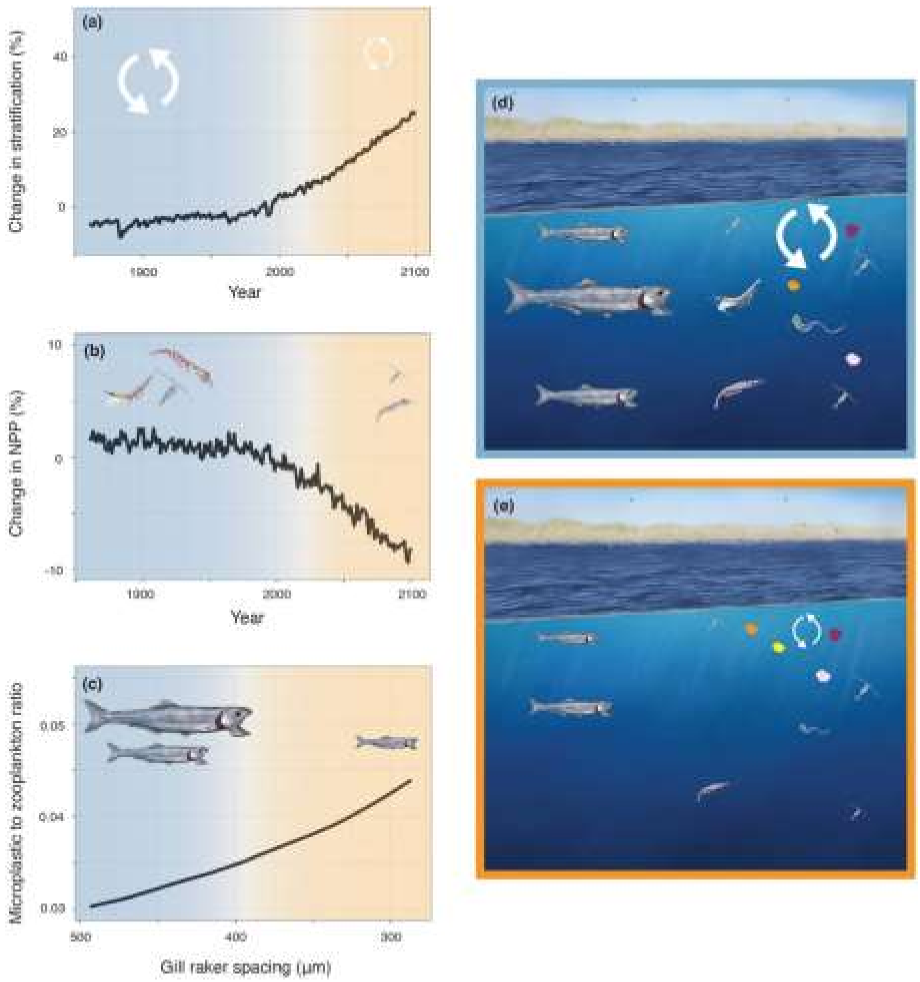

Figure 4. Conceptual schematic detailing how projected changes in climate may affect the exposure of forage fishes to microplastics relative to their natural prey in offshore, open ocean regions. (a)–(c) Shading represents projected shifts from the current open ocean ecosystem state (blue) to the future state (orange). (a) & (b) CMIP5 model simulation and projections for (a) increases in stratification, defined as the density difference from 0 to 200 m depth, and (b) declines in net primary, productivity since 1990 [74]. Declines in net primary productivity may reduce the abundance and size of zooplankton individuals available for foraging anchovy. (c) Increase in microplastic exposure for Northern Anchovy with decreasing body size and gill raker spacing. Estimated based on the morphological constraint of anchovy's gill raker spacing on the smallest particle that can be consistently ingested [12]. (d) Current, offshore ecosystem state. Foraging fishes are exposed to zooplankton and positively buoyant microplastics (colored polygons) transported to depth via vertical mixing. (e) Expected future ecosystem state in offshore, open ocean regions. Increased stratification of the global ocean will limit the maximum depth positively buoyant microplastics can be transported to. Declines in productivity will likely decrease the size and abundance of available zooplankton prey. Declines in offshore primary productivity may also decrease both the body size and school size of forage fishes. Plastic pollution will likely increase microplastic availability to forage fishes. Illustration elements by K Lance.

day [68]. The peak of Northern Anchovy spawning is in the late winter—early spring (February—April) [67], corresponding with the peak in relative microplastic exposure for juvenile anchovy. As such, any negative consequences of microplastic ingestion by anchovy may be relevant for future assessments of anchovy recruitment.

Microplastic consumption by anchovies may also have consequences for the predators of anchovy, perhaps through the trophic transfer of microplastics. Anchovies are known to transfer pollutants to their predators, such as sea lions [70]. The potential for bioaccumulation of microplastic pollutants and trophic transfer of microplastic particles to anchovy predators depends on the rate of predation on anchovies and the number and sizes of ingested microplastics [71, 72]. Further investigation into the physiological and behavioral consequences of microplastic consumption on anchovy is necessary before we can fully understand how important anchovies are as a trophic pathway for microplastic cycling within marine food webs.

Other forage fish species may be more susceptible to microplastic ingestion than the Northern Anchovy. For example, Pacific Sardine (*Sardinops sagax*) can consume smaller particles on average than anchovies, preferentially filter feed [66], and are more abundant offshore in the CCE where zooplankton prey are less abundant [56, 64]. The large filtration area of sardines may also increase the number of particles they consume compared to anchovies [15]. Thus, sardines likely have a higher overall microplastic exposure than anchovies in the CCE. While sampling constraints prevented us from investigating sardine microplastic exposure, future studies may benefit from this examination.

3.5. Forage fishes exposure to microplastics with a changing climate

Given our findings and the clear linkages between climate change and marine plastic pollution [73], climate change in the coming century will likely alter the exposure of forage fishes to microplastic particles. Microplastic exposure in anchovies is constrained by (1) near-surface mixing (which transports microplastic particles to depth), (2) primary productivity (which limits zooplankton abundance), (3) anchovy body size (which controls the smallest particle that can be ingested), and (4) microplastic abundance in the surface ocean. Projected changes in global climate will likely alter each of these factors in offshore, open ocean environments, subsequently increasing the relative exposure of forage fishes to microplastics offshore. Although anchovies are typically a nearshore species, other forage fishes such as the Pacific Sardine are found offshore, and may be more affected by relative increases in microplastic exposure [64]. Surface waters in the open ocean (0–200 m) are projected to increase in stratification by up to 30% in the year 2100 [74] (figure 4(a)). Increased stratification will decrease the maximum depth of transport for positively buoyant microplastics, resulting in higher potential microplastic exposure for forage fishes that feed shallowly. Increased stratification of the ocean will also limit the transport of deep, nutrient-rich waters to the surface, reducing primary production on average. Although the impacts of climate change on coastal upwelling systems are not well constrained [75, 76], in the global ocean, net primary productivity is expected to decrease by up to 16% over the next century [74] (figure 4(b)). Lower net primary productivity may decrease the size and abundance of zooplankton prey [56], consequently increasing relative microplastic exposure for zooplanktivorous forage fishes. Lower productivity and prey availability may also decrease the overall body size and abundance of forage fishes in the future [77]. The smaller gill raker spacing associated with smaller anchovies and other forage fishes that filter feed would increase exposure to smaller, more abundant microplastics (figure 4(c)). Finally, marine plastic pollution has increased exponentially, and plastic inputs to the ocean are projected to continue increasing [78, 79](figure 4(c)). Together, future shifts in the physical environment, prey field, fish body size, and plastic concentration will likely increase microplastic exposure for forage fishes that filter feed in the open ocean (figures 4(d) and (e)).

4. Conclusions

Despite a growing literature of marine species ingesting microplastic particles across the global ocean, Northern Anchovy in the CCE had relatively low exposure to microplastics during the sampling period. Microplastics constituted fewer than 5% of all prey-sized items. The highest potential exposure to microplastics was for small, juvenile anchovy (1 year old) foraging offshore, during the day, in the winter. Due to continued increases in microplastic pollution, small forage fishes that filter feed in the open ocean are likely to experience higher levels of microplastic exposure in future global climate scenarios.

Data availability statement

The data that support the findings of this study are openly available at the following URL: https://bitbucket.org/anelachoy/microplastic_exposure_chavarry/src/master/.

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Author contributions

C A C, K L L, and N M B conceptualized research; C A C supervised research and acquired funding; M D O generated data; J M C curated data with assistance from N M B; J M C performed data analysis and visualization with substantial assistance from C A C, K L L, and A D B; J M C wrote the paper; C A C, K L L, A D B, N M B and M D O reviewed the paper.

Appendix A. Figures and tables

'IabkA1, Puamdcn W>Cdin th e depth decay modd to :account for wind drn-cn'\tcrtical mixing of positively buoyant microplartic particl<t.Pu am <tcn co m, &om Kul-ulka etol [: U], Kooi dal (35], Thorp< et al [SQ], and Taylor [SI].

Variab-le	Name	Valu-e	Unit.s	Source
p,,;,	Airden$:lty	Varie.s	kg m •	Cruises 0604 0607 and 0610: CalCOFI Und.crv.•ayData reported air temperatur-e and relative humidity. converted to airdemity bysea-mat in MATLAB. Crui s-e 070 I : Hydrograplm data froma CTDcut at the same$lation recorded dryand wet temperature. Converted to rd ativc humidity using sc--a- m at in MATLAB. then convcrtedagain to airckmity.
I<	von Karman constant	0.4	NIA	Kuku!k.. tal (34]
g	Gravity	9.Sl m-s 2	Kukulka... 1 (34]	
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''''	P lasticrisespeed	0.009	m -a 1	Kooi ,tal (35]
d	Net immerci.on depth	0.155	m	Ca!COFI Report
u,o	W i n d speedat 10 m abovesea.surface	Varie.s	m-s 1	Cruis« 0604. 0607 and 0610: CalCOFIUnd.crv.•ayData win d speedand reported anemometer height converted to U1O usin g c.dnlp fromsea-mat in MATLAB. Crui se 0701: \\Find$peed recorded during a CTD cast. Anemomrter height inferred from a$ketch. Convc-rted to U 10 using cdrtlp fromsea-mat in MATLAB.
•••	Fr ic ti on al air vd oci ty	Jc,Uy.	m - s 1	Th o rp e et al [SO)
H,	Sig nificant wave heigh t	0.96-g 1ui u!.	m	Kuk ulka ... 1 (34]
C ,	D rag cod li cien t	for U 10 <4 = N/A for U10 >4 = **MATLAB** Too lbox Re-$ult	NIA	Cruises 0604. 0607 a.ad0610: CalCOFI Unde rv•.ay Data wind speedand reported anemometer heish t co nvert ed to Cd using c.Jnlp fromsea-mat in MATLAB. Crui se 0701: \\Find$peed recorded during a CTD cast and anemometer height (inf<rredfrom amtchoftheship) were converted to Cd using cdnlp fromsea-mat in MATLAB.
T	Wind streu	c,pwUio	N m 2	Taylor (81]
P.-	,\Tater densi ty	Va.ric-$	kg m •	Hydr ogra phi c da ta recorded .rurface sc--awate-r densi ty during a CTDcart.
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A.	Near-surfuee mixing d u-e to breaking waves	1.5•u .,KH,	m2 s- 1	Kukulka ... 1 (34]
N	Total number of dep th -in tegrated, buo yan t plastic particle$	Nthri:C+::rl 1- .- h Ylo I	#	Kukulka ... 1 (34]

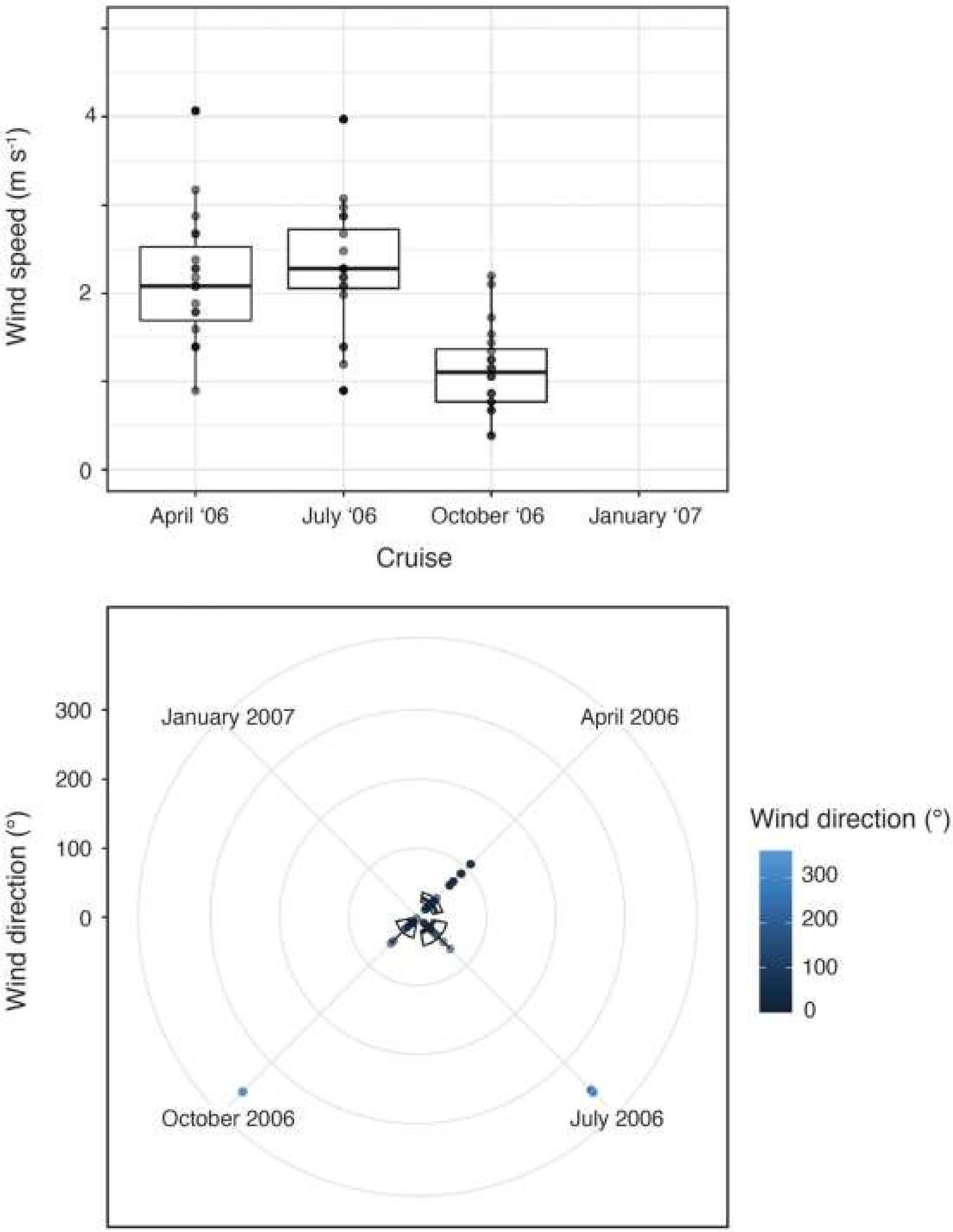

Figure A1. Range in wind speed and direction during surface plastic particle collections *Top*: Range in the wind speed (10 m above sea surface), 10 min before and after recorded plastic particle collection time. Speeds varied by less than 5 m s ^{1} for April, July, and October 2006. *Bottom*: Range in wind direction (degrees) 10 min before and after recorded plastic particle collection time. Changes in wind direction exceeded 50 for $n = 13$ tows. For all other tows ($n = 46$) range in wind direction was less than or equal to 50 . Underway data were not available for January 2007.

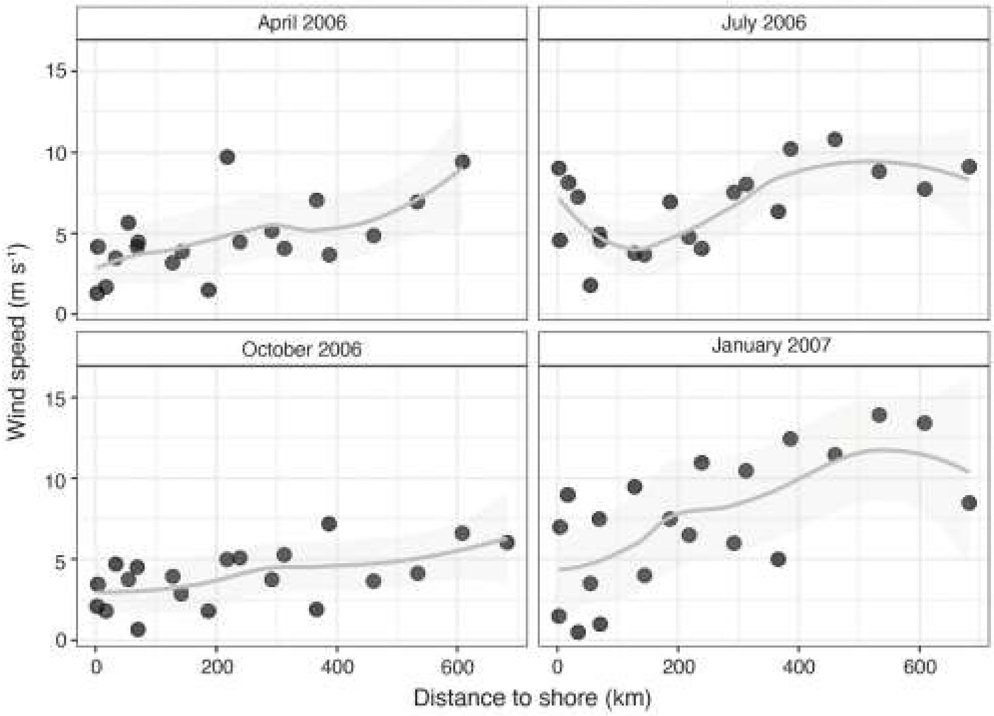

Figure A2. Wind speed (10 m above sea surface) recorded at the time of net tow as a function of increasing distance from shore for all cruises. Distance offshore estimated from the CalCOFI stations closest to land. Curves represent LOESS fits. Shading represents 95% confidence intervals.

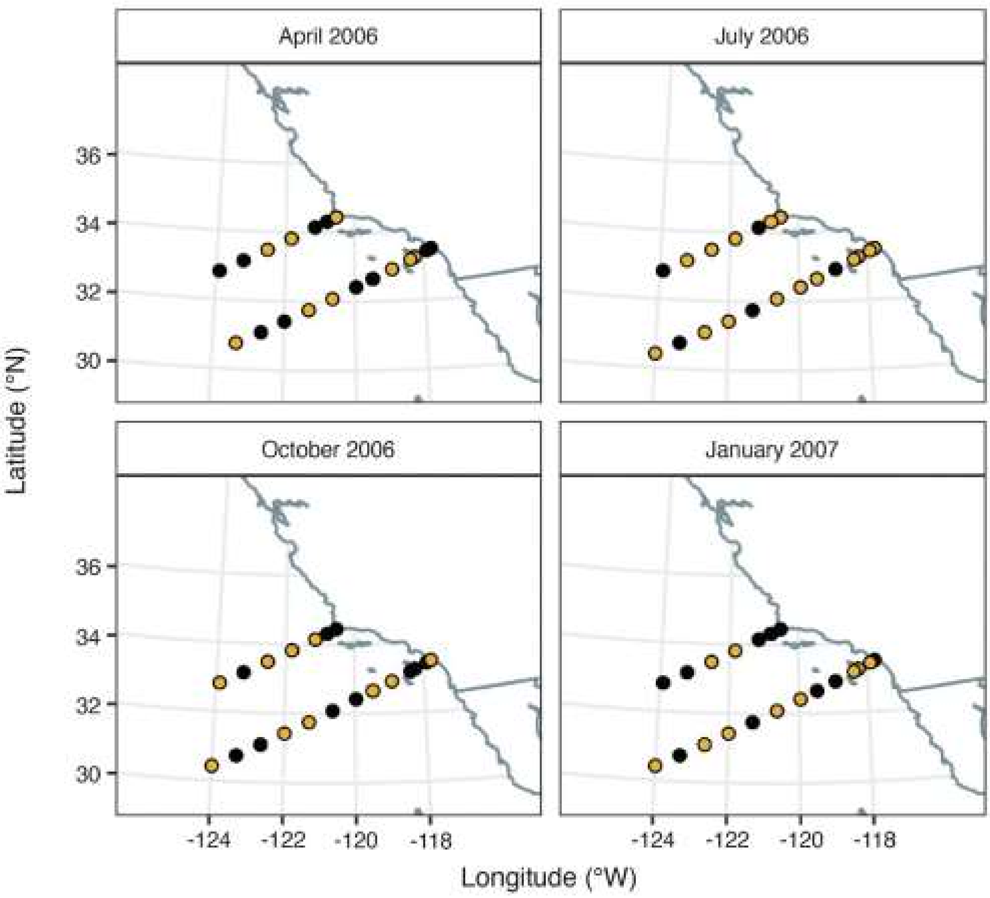

Figure A3. Year and month of zooplankton collections. Filled circles represent day (yellow, n = 44) and night (black, n = 35) tows.

Appendix B. Datasets

All data and analytical code are available in a public repository (see Data Availability statement). Datasets are as follows:

CalCOFIEffort.csv- Data for the general CalCOPI sampling grid. cr11ise-month of sampling. line-GtlCOPI line of sampling. station-CalCOPI station of sampling. *latitude* and *longitude-sampling* location in decimal degrees.

monthly_wind_CCMP.cs-v Monthly-averaged wind speed at 10 m above the sea surfaoe from Atlas *et al* (2011) [28]. time- modeled month. *latit11de* and *longitude-modeled* location in decimal degrees. *wspd-wind* speed (m s $^{-1}$) 10 m above the sea surface.

Ancho vyGillSpacing.csv-Change in anchovy gill raker spacing from Rykaczewski (2009) [12]. *anch_ standard_length_mm-<1I1chovy* standard length in mm. *gill_raker_spacing_mm-<1I1chovy* gill spacing in mm.

ProportionalAbnndancebySize.csv-{: bange in the median abundanoe of microplastics and zooplankton based on particle and pr:ey size. *size_ mm- th e* minimum particle or pr:ey size. *median_zp_abun_m3- the* median abundanoe of zooplankton prey available to a :foraging anchovy (# m •) within the size bin (*:size_mm* + 0.04 mm). *relative_zp--the* median proportion of zooplankton prey available to a :foraging anchovy (%) within the size bin (*size_ mm* + 0.04 mm). *median_plas_ab,m_m3- the* median depth-integrated, size-corrected abundance of microplastic particles available to a foraging anchovy (# m •) within the size bin (*size_r,1m* + 0.04 mm). *relative_pia-the* median proportion of microplastic particles available to a foraging anchovy (%) within the size bin (*size_ mm* + 0.04 mm).

RelExpData.csv- Primary data used in the manuscript. crni.se- mont h of sampling. !ine-CalCOPI line of sampling. *station-CalCOPI* station of sampling. *time_sampzea-..ampling* time, either day or night. *latitude* and *longitude--"..ampling* location in decimal degrees. *surf_plas_avail_per*_m3- the abundanoe of surface microplastic particles within the feeding size range of an anchovy (# m ' }. *depth_in t_plas_avail_per nm3- the* abundanoe of depth-integrated microplastic particles within the feeding size range of an anchovy (# m '). *zoop_am il_per_m3- th e* abundanoe of depth-integrated zooplankton available within the feeding size range of an anchovy (# m '). *ulO_,,,_the* wind speed 10 m above the se-a surfaoe at the time of plastic colleciton (m s $^{-1}$). *di.stance_to_shore_ m- the* clistanoe from the sampling station to shore, where shore is approximated by the CalCOPI station closest to shore (m).

RelExpChangeWithAnchovySize.csv-Ch ange in anchovy exposure with increased anchovy size and gill raker spacing. *gill_raker_ spacing_um- the* mean inter-gillraker spacing (µm). *max_expos,,re_plas_zp -<1I1chovy* maximum exposure to microplastic relative to zooplankton prey.

Fu2016SI.csv-{:MIPS modeled projections for changes in ocean stratification from Fu *et al* (2016) (74]. *strat_perc_change- th e* projected change change in stratification from 0 to 200 m depth in the global ocean sinoe 1990 (%).

Fu2016NPP.csv-{:MIPS modeled projections for changes in ocean net primary productivity from Fu *et al* (2016) [74). *npp_perc_change- the* projected changechangein net primary productivity in the global ocean sinoe 1990 (%).

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