

Research Article

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Partial migration in diadromous fishes drives the allocation of subsidies across the freshwater-marine ecotone

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Abstract: Migratory animals can act as cross-boundary subsidies sustaining ecosystem functioning, such as diadromous fishes that migrate between fresh water and seawater and carry nutrients and energy across the freshwater-marine ecotone. Frequency and timing of migration are however highly variable within and among populations. We hypothesized that in catadromous fishes (i.e., diadromous fishes that grow in freshwater and spawn in the sea, such as eels), the import of subsidies by migratory juveniles could outweigh the export of subsidies by adults due to skipped spawning migration. We used the diamond mullet *Planiliza ordensis*, as a model species, and determined life-history traits using a combination of length-to-age data, acoustic telemetry and otolith (fish ear stone) microchemistry. We used a mass balance approach to model individual mass acquisition and allocation, and extended our model to other life-history strategies. Our results showed high intra-population variation of migratory behaviour in *P. ordensis*, with few individuals migrating every year to spawn. We estimated that an individual

P. ordensis acted as a net 42.6g biomass subsidy in fresh water, representing a retention of more than 50% of the juvenile mass at freshwater entry. Our model predicts that skipped spawning is likely to alter the allocation of subsidies in diadromous species, highlighting the important effects of individual variation in migratory behaviour on fluxes of energy and nutrient at ecosystem scales. We encourage future studies to consider how variation in migratory behaviour is likely to affect the direction and magnitude of biomass fluxes across ecotone boundaries.

Keywords: Partial migration; Skipped spawning; Catadromy; Marine-derived nutrients; Prey availability

1 Introduction

Most ecosystems are recipients of allochthonous resources (i.e. not originating in the region where they are found), such as nutrient, organic matter and prey, that enhance *in situ* productivity [1,2]. Recent theoretical and empirical studies suggest that low to moderate allochthonous inputs (or ‘subsidies’) can stabilize trophic dynamics, defined as the movement of carbon, nutrients, and energy among organisms in an ecosystem [3,4]. However, depending on the trophic levels that use the resource, trophic dynamics can become unstable as inputs increase [5,6]. One striking example is when excessive inputs of allochthonous carbon from newly inundated riparian areas during high river flows create hypoxic conditions that can cause large-scale deaths of fish and other riverine organisms, and thus the loss of the steady state [7,8]. Similarly, the transfer of large amounts of organic matter from agricultural activity into natural ecosystems can fundamentally alter trophic dynamics: trophic cascades can be initiated and rare or uncommon species can become invasive while functionally important common species decline [9]. Such examples demonstrate the sensitivity of ecosystems to

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variation in the direction, extent and biochemical pathways associated with subsidies [10].

Migratory animals transport vast amounts of energy and nutrients assimilated in body tissues or as waste products (e.g., faeces, urine) across ecotone boundaries [11]. This holds particularly true for diadromous fishes (i.e., fish migrating between seawater and fresh water, such as salmon and eels), which connect marine ecosystems and inland waters via subsidies. One iconic example is the migration of Pacific salmon (*Oncorhynchus* spp.) that subsidize streams with marine-derived biomass [12], which sustain lotic and riparian ecosystem functioning [13]. There is increasing evidence that other diadromous fishes also act as important fluxes of energy and nutrients. For instance, Engman, Kwak, and Fischer [14] have estimated that the mass migration of tiny diadromous goby larva (~0.1g each) import a ton of marine-derived biomass per migration event to a single river because they migrate by millions, representing a significant input of biomass to the stream. Diadromous fishes include catadromous and anadromous species that use the freshwater and marine ecosystems, respectively, as a growing biome and, marine and freshwater ecosystems, respectively, as a breeding biome [15]. In addition, diadromy also includes amphidromy that can be considered as an extension of catadromy in which larva drift to the ocean instead of spawner migration [16]. Ontogenetically, diadromous fishes contribute unequally to fluxes: for example, adult Pacific salmon accumulate most of their mass in the ocean (> 95%, [12]) and typically weigh one-to-two orders of magnitude more than out-migrating smolts (e.g. 12g vs 5.5kg see [17]). Thus, the direction of spawning migration has been proposed as the main driver of nutrient flux, with anadromous and catadromous fishes expected to represent a gain and a loss of nutrients and energy for freshwater ecosystems, respectively [18].

An emerging theme in research on migratory animals over recent decades, particularly with the advent of telemetry and other methods that provide detailed information on the movement of individuals, is the high incidence of resident individuals within migratory populations, a phenomenon referred to as partial migration [19]. Skipped breeding partial migration is one type of partial migration when resident individuals forgo breeding migration some years. In diadromous fishes, this is the case when mature individuals skip spawning, as reported for several species, such as sturgeons (*Acipenser brevirostrum*, [20]), salmonids [21,22] and barramundi (*Lates calcarifer*, [23]). Skipped spawning is a common strategy in fish [24,25] that provides fish with the ability to maximize their adult individual fitness in response to

ambient conditions by delaying the timing of reproductive investment until more suitable conditions occur [26,27].

It is increasingly recognised that partial migration can affect trophic dynamics in ecosystems [18,28,29]. For instance, the proportion of migrating cyprinids from lakes to streams affect the predator community structure [30] and may drive the steady state of lakes by a top-down control on plankton [31]. However, little is known on how partial migration influences the fluxes of energy and nutrients between the freshwater and marine ecosystems. In the current study, we hypothesized that skipped spawning in diadromous fishes could be a main force driving the allocation of subsidies across the marine-freshwater ecotone. We used the catadromous diamond mullet, *Planiliza ordensis*, an important prey species in riverine food webs of Northern Australia, as a model species. We considered subsidies in the form of prey availability, given the importance of mullets as prey for predators in both environments. Analysis of otoliths (ear bones that act as natural record of growth and migratory pattern), population surveys, and acoustic telemetry were used to elucidate individual life-history traits such as timing of migration, mortality, growth and migration frequency. We applied our findings to estimate biomass fluxes across the freshwater-marine ecotone, and then explored our model with regards to variation in life-history traits. Specifically, we explored how skipped spawning in other diadromous fishes could affect the allocation of biomass between the freshwater and marine environment.

2 Material and methods

2.1 Study species and study system

Planiliza ordensis (Family Mugilidae) is endemic to Northern Australia [32,33]. It grows to a maximum size of ~500 mm total length (TL) and has a detritivorous-herbivorous diet [34]. Collection of large numbers of juveniles in the lower reaches of the Daly River, Northern Territory, Australia after the wet season (King, A. unpub data) and recent otolith chemistry analyses demonstrate migration from saline to fresh water [35] confirming a catadromous life history as reported by [36]. Gonad maturation occurs in fresh water, and stable isotope analysis suggests that food source do not vary seasonally [37]. *P. ordensis* could be considered as semi-catadromous as it is unclear if adults spawn in the estuary or in the ocean [34]. *P. ordensis* is an important prey species for high-order predators in Northern Australian rivers, including teleost

fishes (e.g., barramundi *Lates calcarifer*, forktail catfishes *Neoarius* spp.), euryhaline elasmobranchs (bull shark *Carcharhinus leucas*, northern river shark *Glyphis garricki*), the estuarine crocodile *Crocodylus porosus* [38] and piscivorous birds (e.g. white bellied sea eagle *Haliaeetus leucogaster*, eastern great egret *Ardea modesta*, Whistling Kites *Haliastur sphenurus*) [39]. Given its catadromous life history and its importance in food webs, *P. ordensis* likely acts as an important cross-boundary subsidy, sustaining predators in rivers [40].

The study was conducted in the Daly River (DR) and South Alligator River (SAR), Northern Territory, Australia. The region is a tropical savannah characterized by a monsoonal climate with distinct wet and dry seasons. Rainfall is extremely seasonal, with 95% falling in the wet season between October and May (Australian Bureau of Meteorology), driving high river flow and vast highly productive floodplains [41]. The main channels are considered oligotrophic and heterotrophic [42].

2.2 Fish growth and migratory pattern from otoliths

2.2.1 Otolith collection and preparation

For otolith ageing and microchemistry, individuals were collected and euthanized from the DR, in the late dry season/early wet season (Jul.-Oct) 2012-2013 ($n=47$; 88-395 mm standard length (SL), 18.1-1768 g) and wet season (Jan.) 2014, from the SAR ($n=25$; 240-380 mm SL, 244-1358 g) (Fig. 1). Fish were sampled by boat electrofishing from the main river channels, far upstream (70-120 km) the estuary mouth and thus representing freshwater dwellers. Upon capture, fish were immediately euthanized by overdose in Aquis (175 mg L⁻¹ 1242) and measured and weighed to the nearest mm and g, respectively. The sagittal otoliths were removed in the field and placed into labelled paper envelopes for storage prior to preparation for analysis. Otoliths are calcified structure of the inner ear of fish, made of successive layers of calcium carbonate and proteins that act as a record of growth and environmental conditions experienced by fish [43]. Otoliths are characterized by annual increments due to seasonal variation in metabolism which provide the ability to age fish and back-calculate growth [44]. As the otolith grows, its composition also reflects the environmental water chemistry. In particular, ratios of strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$) are indicative of experienced water salinity [35,45]. In preparation for analysis, one sagittal otolith from each fish was embedded in two-part epoxy resin (EpoFix; Struers, Ballerup, Denmark) and

transversely sectioned to a thickness of 300 μm through the primordium using a low-speed saw. The sections were polished using lapping film (9 μm), rinsed with deionised water, air dried and mounted on glass slides using epoxy resin. We used fish otoliths to infer fish growth, age and length at freshwater entry, and spawning migratory pattern (see below).

2.2.2 Otolith ageing for fish growth and mortality estimation

For otolith ageing, annual growth increments were identified according to previous studies on other mullet species [46,47] and measured along the otolith chemistry transect under 100X magnification using a stereomicroscope and image analysis software (Image-ProPlus, ver 4.2, Media Cybernetics, Rockville, MD, USA). The relationship between age and SL was analysed using the von Bertalanffy equation of the type $\text{SL}(t) = \text{SL}_{\text{max}} \cdot (1 - e^{-K(t-l)})$ where SL_{max} is the maximum SL of the fish, K is the growth coefficient, l is the time reference and t is the fish age [48]. The model was fit using the function *nls* in R (Additional material: Fig. S1, $R^2 = 0.71$) and we found $l = 0.32$, $K = 0.332$ and $\text{SL}_{\text{max}} = 500.1$ mm. We used a function of the type $W = a \cdot L^b$ [49] to examine the relationship between SL and body mass of aged fish, where W is the weight, L is the standard length, a and b are species-specific parameters. We did not find differences in residuals between sexes (one-way ANOVA including males, females and juveniles, $F = 0.79$, $P = 0.46$) or sites (one-way ANOVA, $F = 1.9$, $P = 0.10$), suggesting no effect of sex on growth trajectory. Data were log-transformed and examined with least squared regression (Additional material: Fig. S2, $R^2 = 0.99$). Combining the two models, weight-at-age was described by:

$$(1) W(t) = a \cdot (1 - e^{-K(t-l)})^b$$

2.2.3 Migratory patterns based on otolith microchemistry

A multi-collector laser ablation-ICP-MS was used to measure Sr isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) from the core to edge of transversely sectioned sagittal otoliths following the methods outlined in [35,50]. Four fish were removed from the analysis because examination showed that the laser transect did not traverse the primordium due to sample preparation issues. An algorithm was used to consistently

determine the timing of freshwater entry based on the $^{87}\text{Sr}/^{86}\text{Sr}$ transect data for each fish following three criteria: (i) $^{87}\text{Sr}/^{86}\text{Sr}$ ratio above 0.7096, corresponding to a salinity of $<5 \text{ g.L}^{-1}$ in both rivers [23,35]; (ii) a local increase of $^{87}\text{Sr}/^{86}\text{Sr}$ ratio corresponding to a migration into less saline water; (iii) and an increase in the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio ($>2\text{‰} / 50 \mu\text{m}$ of transect) indicating sustained fresh water residence (Fig. 2). We examined the relationship between otolith core-to-edge transect distance and fish SL (mm) and weight (g) with least squared regression, assuming linear and log-linear relationship, respectively, in this range of size (Additional material: Fig.S3, $R^2 = 0.76$) [51]. The analysis included a broad range of fish size (88–375 mm SL)

to ensure that the model was biologically relevant [52]. We used those relationships to back-calculate the length and weight of fish at freshwater entry. We identified migration to brackish water by visually identifying portions of the $^{87}\text{Sr}/^{86}\text{Sr}$ transects that were below or close to the value of 0.7096 (Fig. 2). This value corresponds to a salinity of at least 5 g.L^{-1} during the wet season, according to previous sampling and mixing models in the DR [35], and the SAR [23]. In both rivers, $^{87}\text{Sr}/^{86}\text{Sr}$ show little change above 2 g.L^{-1} , and a sharp decrease in otolith $^{87}\text{Sr}/^{86}\text{Sr}$ is indicative of a transition to brackish waters.

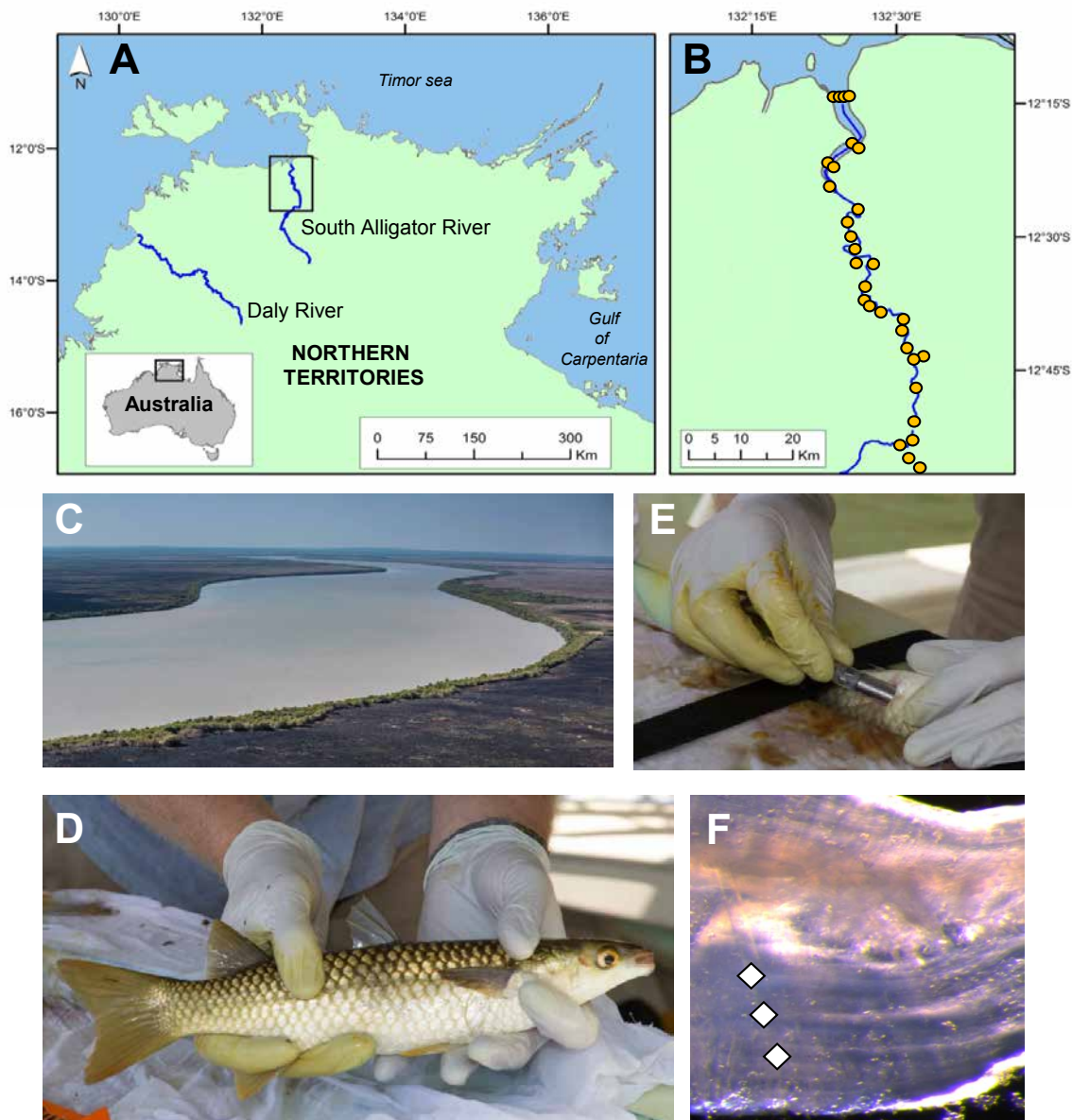


Figure 1: (A) Map of the study area. (B) Zoom in the South Alligator River, orange circles show acoustic antenna locations, down to the estuary. (C) Aerial photography of the South Alligator River. (D) Photography of *Planiliza ordensis*, (E) shows the surgical implantation of an acoustic transmitter. (F) Example of a core-to-edge otolith transect. Diamonds show the location of annual rings.

2.3 Individual survival based on population survey

As part of another study, 929 *P. ordensis* were surveyed biannually in both the early and late dry season, over a 7-year period from 2006–2012 in the DR catchment. A complete description can be found in Keller *et al.* 2019. In brief, fish were sampled at discrete multiple locations (shots or replicates) using a boat or backpack electrofishing (pulsed DC), depending on water depth. Electrofisher settings were adjusted to maximise efficiency of collecting fish with minimum power. At least 15 electrofishing shots of five minute elapsed duration were undertaken for each sampling event, and shots were stratified to ensure each available habitat type within each site was sampled at least once. Prior examination of sampling efficiency has revealed that 15 shots yields an accurate estimate of species composition and assemblage structure within each site (Kennard *et al.* unpubl. data). Electrofishing shots were conducted in as homogenous area as possi-

ble and averaged 77 m (± 48 SD) in length (range = 5–263 m). At the completion of each electrofishing shot, fish were counted and measured (SL) to the nearest mm, and returned alive to the point of capture.

We used length data to ensure that the back-calculated size at freshwater entry determined by otolith microchemistry was consistent with field data. We also used those data to infer mortality in fresh water. As length did not significantly differ between years (see Results), this effect was not further considered. We used the von Bertalanffy equation that we established with otolith ageing (see above) as an age-length key to transform fish length to age and estimate population age structure [55]. As the size structure did not differ between early and late dry season (see Results), we pooled all age data by normalizing age structure to early dry season. We assumed that fish under 2 years were under-estimated due to sampling bias; thus, we calculated disappearance for fish >2 years as the proportion of fish missing between an age class and the subsequent one.

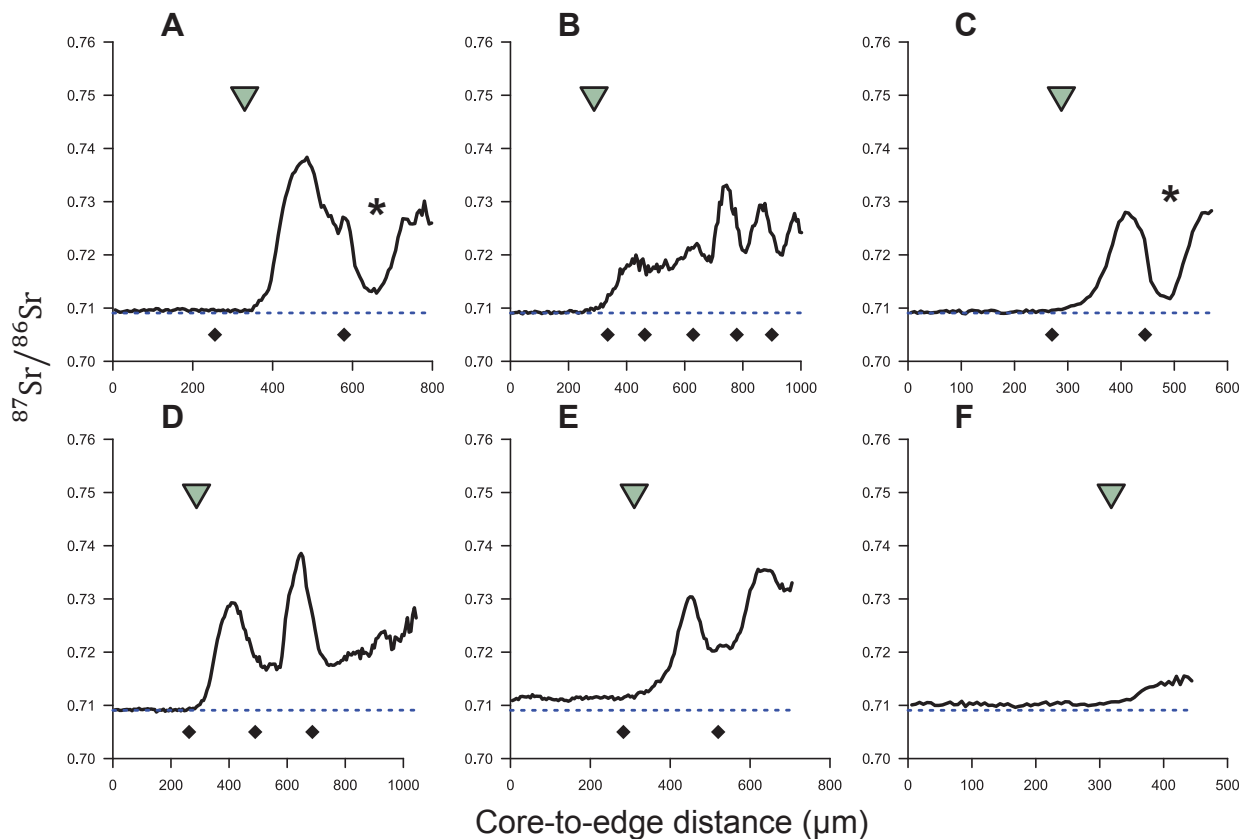


Figure 2: Example of core-to-edge transect of otolith $^{87}\text{Sr}/^{86}\text{Sr}$ in individual *P. ordensis* from the Daly River (A-D) and South Alligator River (E-F). Blue dotted lines show the marine value of $^{87}\text{Sr}/^{86}\text{Sr}$. Black diamonds show the location of annual increments. Green triangles show the predicted location of freshwater entry (see Methods). The two stars show example of seaward spawning migrations.

2.4 Adult spawning behaviour and mortality from acoustic tracking

Data from 25 *P. ordensis* that were tracked in the SAR using acoustic telemetry were used to directly monitor movements of fish into the putative spawning grounds and derive a second, independent mortality rate estimate for comparison with the estimate from population age structure [56]. Fish were collected by boat electrofishing and tagged by surgically implanting acoustic transmitters (Vemco V13, 36 mm length, 11 g, 695 days estimated battery life, Vemco, Nova Scotia). Fish were adults, between 300–370 mm standard length (SL), mean 336 (± 21 SD) mm SL. A complete description of the tagging method is provided by [23].

An array of 30 acoustic receivers was deployed from the freshwater reaches of the SAR to the estuary mouth (Fig. 1). As detections of all fish were contained within the region covered by the acoustic receiver array, disappearance of telemetered fish within the battery life of the transmitters was assumed to reflect mortality [57]. The sudden cessation of detection is a strong indicator of mortality [58], as the only alternative hypothesis would be tag expulsion (which usually occurs shortly after tagging [59]) or tag malfunctioning (which is not expected [60]).

We calculated the mortality rate using a full year of acoustic data from October 20th 2013 to October 20th 2014. Survival was computed using the function `survfit` in the package *survival* [61], using the `tsiatis` method to estimate survival error [62]. Ten of the 25 tagged mullet were not detected during the study, suggesting mortality in the immediate post-tagging period; possibly due to the relative sensitivity of the species to handling and the harsh environmental conditions at the time of collection and tagging (water temperature $>34^{\circ}\text{C}$, dissolved oxygen $<1\text{ mgL}^{-1}$). The remaining 15 fish exhibited wide-ranging movements and we assume there were no long-term tagging effects for these fish [63]. One fish was last detected at the furthest upstream antenna, and thus we could not determine its fate and we did not include it in the survival analysis.

2.5 Statistical analysis

All data analysis, statistics and modelling were done in R version 4.0.2 [64].

To test for effect of sex on skipped spawning rates, effect of sex and size on weight-to-length relationship residuals, and effect of seasons and years on age frequency, we performed one-way ANOVA tests. For each

test, we checked normality of data (Shapiro-Wilk tests and Q-Q plots).

2.6 Allocation of subsidy modelling

We modelled the mean net biomass flux to freshwater that was driven by an individual *P. ordensis*, using an individual mass balance approach, considering biomass that was acquired in one biome and delivered to the other biome. Given that diamond mullet mature in freshwater [37] and that movement in the marine environment is limited (see Results), we considered that most of biomass was delivered in the form of prey. Therefore, we only considered subsidy in the form of fish biomass as prey or carcasses for scavengers (i.e. did not consider excretions), and considered that fish disappearance was indicative of predation given the high abundance of predators and scavengers in the system. The model only considered the delivery of allochthonous biomass, therefore not considering juveniles that never migrated to fresh water and freshwater-derived biomass of fish that died in the river, which corresponds to organic matter turnover. We assumed negligible effects of growing during spawning residence in the marine environment, meaning that marine-derived biomass was only acquired before freshwater entry. We defined the freshwater-marine ecotone as the limit between inland water and the estuary.

Thereby, net subsidy into fresh water (S) was calculated as the difference between the flux of marine-derived biomass of fish dying in freshwater (Φ_f) and the flux of freshwater-derived biomass of spawners dying in seawater (Φ_s):

$$(2) S = \Phi_f - \Phi_s,$$

With Φ_f corresponding to the mass at freshwater entry (W_{fentry}) that is effectively delivered to fresh water by fish that die in freshwater, and can be defined as a gross subsidy into freshwater:

$$(3) \Phi_f = \int_{T_{fentry}}^{T_m} P(t)_{death} \cdot P(t)_{alive} \cdot (1 - P(t)_{migrating}) \cdot W_{fentry} dt$$

And Φ_s corresponding to the mass derived from freshwater that is effectively delivered to seawater by spawners that do not return from spawning:

$$(4) \Phi_s = \int_{T_f}^{T_m} P(t)_{death} \cdot P(t)_{alive} \cdot P(t)_{migrating} \cdot (W(t) - W_{fentry}) dt$$

$P(t)_{death}$, $P(t)_{alive}$, $P(t)_{migrating}$ and $W(t)$ are the probability of dying, being alive, migrating (i.e. being in seawater), and weight at age t , respectively. T_{fentry} , T_f and T_m are the age at freshwater entry, first and last spawning migration, respectively. W_{fentry} is the weight at freshwater entry, which corresponds to the biomass derived from seawater..

We assumed that mortality was independent of time of the year, age and habitat (see Results). Therefore, S was simply calculated as:

$$(5) \quad S = W_{fentry} - (1 - ss) \cdot P_{death} \cdot \Delta t_s \int_{T_f}^{T_m} (1 - P_{death})^{t-1} \cdot W(t) dt$$

Where ss is the skipped spawning rate, P_{death} is the annual mortality and Δt_s the time spent in the estuary. The equation corresponds simply to the marine-derived biomass that is imported into fresh water by migrating juveniles (W_{fentry}) subtracted by the biomass $W(t)$ that is exported by spawners $(1 - ss)$ that are still alive at time t $((1 - P_{death})^{t-1})$ and die in the estuary ($P_{death} \Delta t_s$), throughout life of adult fish (integral from T_f to T_m). The equation was computed numerically using a daily increment. Table 1 summarizes how the different parameters have been inferred.

2.7 Model extension to other diadromous fishes

The model was used to investigate how migratory behaviour (age at first migration and skipped spawning) of other diadromous fishes might affect nutrient fluxes, in relation to annual mortality and growth coefficient, two parameters which are subject to broad variations among systems due to external influences [65,66]. The model extension is based on the premise that diadromous fishes use one biome for growth, and the other biome to spawn and grow as early juveniles, therefore excluding feeding in the spawning biome and omitting excretions in the spawning biome for simplification. For the purposes of this exploratory modelling exercise, key life history traits were held at the same value (maximal age fixed at 10 years; maximal weight fixed at 10 kg; same growth model (equation (1)); constant mortality) so that predicted subsidy differences only reflect migration behaviour differences.

3 Results

3.1 Migratory patterns of *P. ordensis*

Estimated fish ages ranged from 1 to 6 years, with a mean of 2.9 years (SD=0.9). In the DR, the seasonal oscillations in $^{87}\text{Sr}/^{86}\text{Sr}$ ratio between 0.72 and 0.73 (characteristic of the main channel, see [35]) matched with annual increments and $^{87}\text{Sr}/^{86}\text{Sr}$ in between the primordium and the first increment were very close to the marine value of 0.70907 [67], confirming marine residence in the juvenile phase and catadromy (e.g. Fig. 2). Of the 68 fish examined, 66 (97%) showed a clear transition in otolith $^{87}\text{Sr}/^{86}\text{Sr}$ from marine to fresh water (Fig. 2). The two fish which did not exhibit such a transition were small fish (<125 mm SL) and had likely migrated into fresh water just prior to capture, leaving insufficient time for incorporation of the freshwater chemical signature (see [68]); in these cases the core-to-edge distance was taken as freshwater entry. Age at freshwater entry ranged between 0+ year (44% of individuals) and 1+ year (56%). Back-calculated SL at freshwater entry was normally distributed (Shapiro-Wilk test, W-statistic=0.98, P=0.39), with a mean of 147 mm (SD=26) (Fig. 3A). This corresponded to an individual mass of an average 72.8g ([62.8, 82.8] 95% CI). Length-frequency data were consistent with the estimated size at freshwater entry from otolith back-calculation, with only two fish <90 mm SL recorded from freshwater (Fig. 3C).

Otolith chemistry revealed few migrations into the marine environment (14 % of fish between 2 and 3 years N=43, 0% of fish beyond 3 years N=9; Fig. 2A, C). The acoustic telemetry showed that five of the 10 fish still being tracked after the late wet season had migrated downstream into the putative spawning grounds downstream the lower estuary (Fig. 4A). Residence times of some migrating fish in the lower estuary were very short (only a few days), which may explain the lower number of migrations detected by otolith chemistry analysis: short-term migrations can be difficult to detect using otolith chemistry due to the laser spot size and time taken for otolith chemistry to reach equilibrium with the ambient water [68]. Nonetheless, both the otolith chemistry and acoustic tracking data suggested a high proportion of skipped spawning each year. Altogether, our data showed a high skipped-spawning rate (~50% and 85% from telemetry and otolith chemistry, respectively) and for the purposes of modelling, we used an annual skipped spawning rate of 50% for *P. ordensis* (Table 1). We also assumed that fish spent an average of 4 months in the estuary based on

our telemetry and otolith data, and previous studies [34] (Table 1). Although sample size was low ($n=35$), the otolith chemistry data suggested no bias in skipped spawning rates among sexes for mature individuals (one-way ANOVA, $F = 0.09$, $P = 0.76$).

3.2 Mortality of *P. ordensis*

Age frequency data for the DR did not differ between years (one-way ANOVA, $F = 1.84$, $P = 0.2$) and seasons (Fig. 3C, one-way ANOVA, $F = 0.63$, $P = 0.46$), and thus was modelled as an age-independent disappearance rate of ~60% for fish > 2 years of age (Fig. 3D). Otolith $^{87}\text{Sr}/^{86}\text{Sr}$ ratio signatures in the same system suggested that no emigration from another system (such as tributaries) occurred for fish

beyond 2 years [35], supporting that disappearance was reflective of mortality.

Tagged fish were detected frequently by the passive acoustic receiver array, with average delays between detections of 2.5 hours and the maximum time between detections averaging 41 days (min = 1 d, max = 110 d). This frequency of tag detection, the lack of detections on the most downstream loggers in the system for most fish, and the estimated tag battery life of ~2 years, all support our assumption that fish that were undetected for >1 year had suffered mortality within the system. The acoustic tracking showed a relatively constant rate of decrease in the number of tagged individuals detected throughout the year (Fig. 4B), suggesting that time of the year (i.e., seasons) did not strongly affect the mortality rate. Although the number of individuals was low, estimates of annual mortality from the acoustic telemetry were high

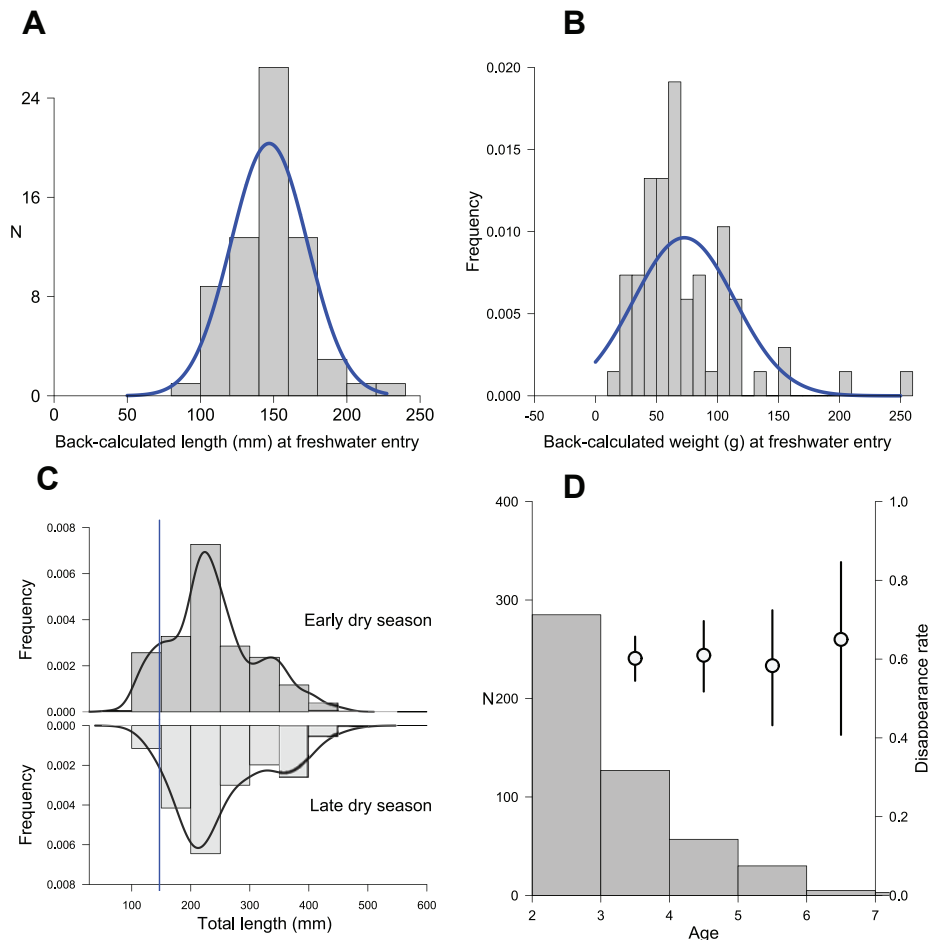


Figure 3: (A) Distribution of back-calculated length at freshwater entry of *P. ordensis*. Blue line shows the normal distribution of the data. (B) Distribution of back-calculated weight at freshwater entry of *P. ordensis*. Blue line shows the normal distribution of the data. (C) Length distribution of *P. ordensis* from the Daly River, obtained by biannual sampling in 2012 (King A., unpub. data.). Blue line shows the mean back-calculated length at freshwater entry. (D) Age structure of *P. ordensis* > 2 years. Open circles show the calculated disappearance rate between age classes. Bars show 95% confidence interval of disappearance rate.

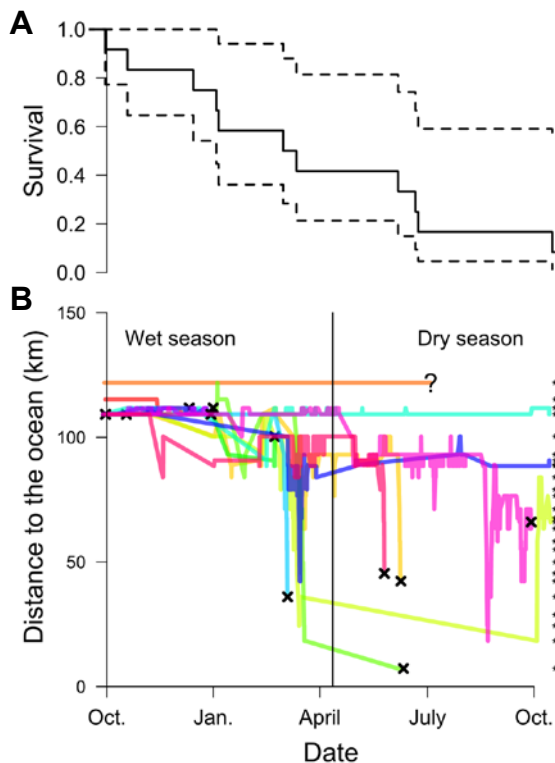


Figure 4: Acoustic telemetry tracking of 15 *P. ordensis* over one year in the South Alligator River. (A) Survival estimate against time. Dashed line denotes 95% confidence estimate. (B) Location of detection events, each colour showing one individual. Stars (on the right) show the locations of acoustic antennas. Crosses show estimated fish death (loss of record, see Methods). Question mark “?” denotes uncertain fate of the fish (death or upstream migration).

at around 80% ([0.45, 0.96] 95% CI) which overlapped with the estimate from age structure. Altogether, our data suggest a relatively constant, age- and habitat-independent mortality rate of approximatively 60-80% per year (Table 1).

3.3 Allocation of subsidies

The maximum subsidy per individual to fresh water corresponded to the mass at fresh water entry ~ 72 g that was estimated from otolith back-calculation and supported by population survey data (Fig. 5). Before the first spawning migration, 80% of this flux was effectively delivered to freshwater food webs due to high mortality, corresponding to gross flux to fresh water. Despite the fact that mature individuals weigh much more than juveniles at fresh water entry, the flux from fresh water to seawater was dampened by the low survival, the relatively high probability for adults to return to fresh water (i.e. iteroparity) and

the low proportion of migrating individuals (i.e. skipped spawning). Skipped spawning was a strong factor affecting subsidy allocation. For an annual skipped spawning rate of 50% -which appears realistic in this population, see above-, we estimated that each mullet represented a net 42.8g flux into fresh water (Fig. 5). However, absence of skipped spawning would result in near-null balance of fluxes with almost as much biomass exported as imported in freshwater (net flux to fresh water of just 12g).

3.4 Predictions for other diadromous fishes

Extending the model to other life-history traits showed that catadromous fishes could allocate a net biomass flux to either marine or freshwater habitat (Fig. 6). Skipped spawning rate was an important driver of the allocation. Populations with low skipped-spawning rate (i.e. most of individuals migrate every year) could only represent a net flux into fresh water under high mortality that prevented most of individuals from growing to large size and exporting biomass when migrating to spawn. In populations with high skipped-spawning rates, the export of biomass remained limited, generally resulting in a net subsidy for freshwater ecosystems. In that case, the magnitude of the subsidy depended mostly on the mass at freshwater entry, which was determined by growth and age at freshwater entry, while mortality had limited influence because most of individuals died while in freshwater.

Given that catadromous and anadromous fishes are broadly symmetrical, the direction of the biomass flux was inverted in the case of anadromous fish. Populations of anadromous fish with high skipped-spawning rates could only act as a net import of biomass to fresh water if juveniles migrate early to the seawater, grow fast in the marine environment and there is high survival (Fig. 6).

4 Discussion

4.1 Prevalence of skipped spawning

There is growing evidence that migration is a highly variable phenomenon at the individual level [69], and Thomson noted many decades ago that populations of a catadromous mullet, *Mugil cephalus*, were composed of individuals forgoing seaward spawning migration [70]. Otolith microchemistry further confirmed high prevalence of skipped spawning in *M. cephalus* with some individuals staying in fresh water for extended periods (>7 years) [71].

Table 1: Parameter estimates used to model nutrient fluxes in the study.

Parameter	Estimate	Parameter (Equation)	Method
Length-weight relationship	$\log(a)=-11.0, b=3.05$	a, b (1)	Fish collection
Size parameter	0.32	l (1)	Otolith ageing
Growth rate	0.332	K (1)	Otolith ageing
Maximum length	500.1 mm	SL_{max} (1)	Otolith ageing
Weight at freshwater entry	72.8g	W_{fentry} (5)	Otolith microchemistry, fish survey
Age at first spawning	2 years	T_f (5)	Otolith microchemistry, acoustic telemetry
Maximum age	7 years	T_m (5)	Fish survey
Mortality rate	$0.6 \cdot year^{-1}$	$P(t)_{death}$ (5)	Fish survey, Acoustic telemetry
Time in the estuary	4 months	Δt_s (5)	Acoustic telemetry
Skipped spawning rate	~50%	ss (5)	Otolith microchemistry, Acoustic telemetry

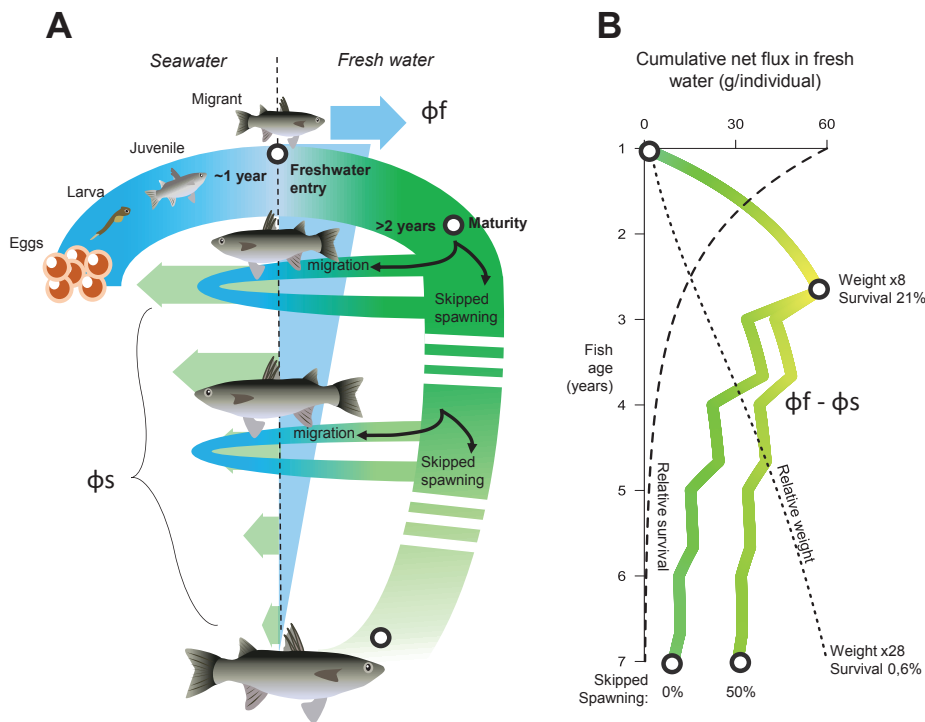


Figure 5: (A) Life history of *P. ordensis*, as inferred from otolith microchemistry, age-at-length data and acoustic telemetry. Φ_f (Flux into fresh water, blue arrow) and Φ_s (Flux into seawater, green arrows) represent the flux of biomass across the freshwater-marine ecotone, as calculated in equation (3) and (4). (B) Dashed line: relative survival after freshwater entry, dotted line: relative weight, continuous line: net cumulative flux in fresh water. After freshwater entry, migrating juveniles start to be preyed in the river resulting in a positive net cumulative flux from the marine to the freshwater environment. Before the first spawning migration, around 80% of mullets have been preyed, meaning that 80% of the mass at freshwater entry (73 g) has been delivered to the river food web. After maturation, the flux is inverted as individuals start to migrate and some do not return from seawater. Older individuals contribute relatively less to fluxes as the increase in biomass is outweighed by the decrease in survival, given our parameters. With increasing proportion of individuals migrating (skipped spawning from 0% to 50%), fluxes to seawater proportionally increase. The net flux of subsidies into fresh water is the cumulative net flux at final age, which is the sum of a continuous incoming flux after freshwater entry -as all individuals derive some mass from their marine phase- and outgoing fluxes at spawning migration –driven by much fewer individuals of bigger mass.

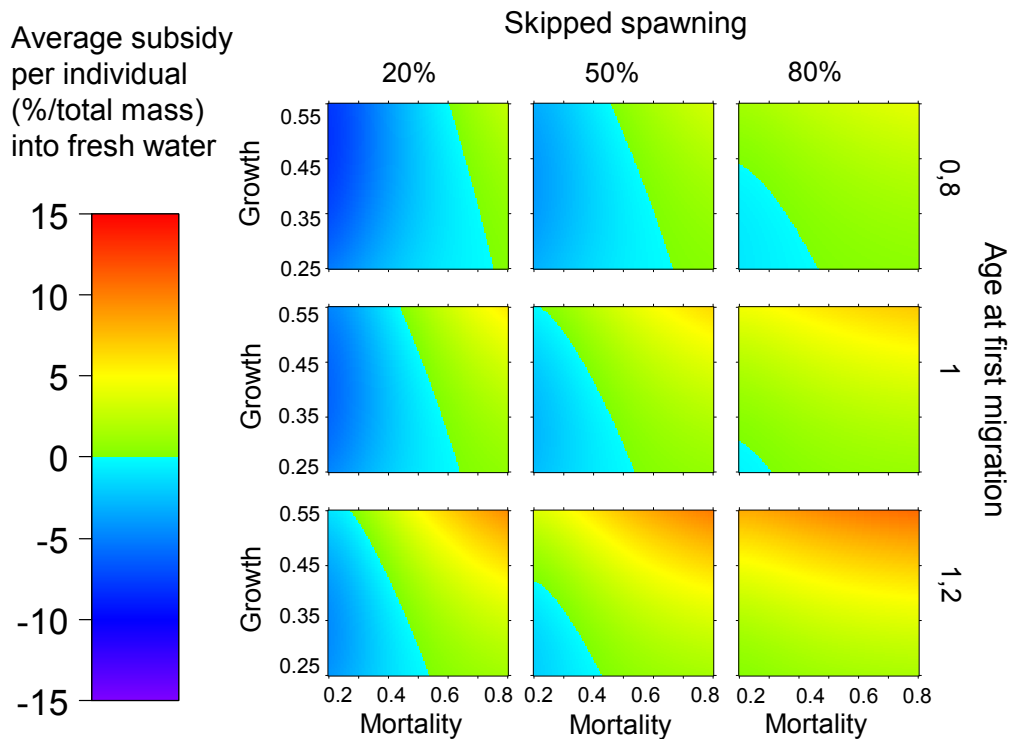


Figure 6: Modelling of the allocation of subsidies across the freshwater-marine ecotone driven by an iteroparous catadromous fish, according to intra-variation life history (see Methods). Skipped spawning increases from the left to the right and age at first migration from the top to the bottom. For a given skipped spawning and age at first migration (i.e. within an individual square), mortality increases from the left to the right and growth from the bottom to the top. Shade of colour shows the direction and magnitude of subsidy in fresh water (kg) for a hypothetical fish that could reach 10 kg at a maximum age of 10 years (see legends). Given that catadromous and anadromous fishes play symmetrical roles, the direction of the biomass flux is simply inverted in the case of an iteroparous anadromous fish.

In line with these studies, our study of *P. ordensis* showed that only a subset of mature individuals migrated every year to the spawning grounds. Skipped spawning can be explained by a trade-off between the benefit and cost of spawning over the long term, as individuals can maximize their cumulative reproductive output by skipping breeding, reducing mortality risk and devoting resources towards growth [24,25]. *P. ordensis* is a capital breeder (i.e. store energy for latter reproduction [72]) which accumulates fat during the wet season in productive floodplains and allocates this energy for reproduction during the dry season [37]. In the case of migratory fishes, skipped spawning might be especially common because of the mortality risk and energetic costs associated with migration [26]. In our study, we could not clearly conclude from telemetry if mortality was higher for migrants because some individuals could move downstream without the intention of breeding. The estimated annual mortality rate of ~60% and the observation of high mortality outside the migration period suggest that either very few individuals migrate at high mortality cost, or that the mortality cost of migration is low, which is supported by the observa-

tion of post-spawned individuals by otolith microchemistry (i.e. some fish survived spawning migration). In both cases, telemetry suggested that most fish are preyed upon in fresh water before they reach the estuarine spawning grounds.

4.2 Net import of biomass driven by *P. ordensis*

To our knowledge, this study is the first estimate of the direction of biomass fluxes driven by a catadromous fish across the freshwater-marine ecotone. Using an individual mass-balance approach, we showed that skipped spawning dampened the flux of biomass to the sea, resulting in a net subsidy of on average ~43 g to freshwater ecosystems. This magnitude of subsidy is likely to be important at the ecosystem level as *P. ordensis* is a common prey species for high-order predators in Northern Australian Rivers [33,38], and given observations of massive schools of mullet entering fresh water (authors pers obs.). The allocation of prey to one or another habitat can have bottom-up

effects on predators [30], with far-reaching consequences on ecosystem functioning [73]. This input of marine-derived biomass could carry essential nutrients and energy to sustain high productivity in those ecosystems while being limited in nutrients most of the year [42]. Even small subsidies can play a critical role in ecosystem processes. For instance, the migration of mayflies can increase juvenile salmon growth in a one-to-three ratio and sustain in cool tributaries populations of fish that are key ecosystem engineers [74].

Although our study only considers the net direction of fluxes to identify source and sink across the freshwater-marine ecotone, it should be recognised that the potential effect of subsidies also relies on the quality of energy [75] and delivery pathways within food-webs [76,77]. For instance, marine subsidies can be critical for freshwater ecosystems because of their role in supplying high quality fatty acids [78] or micronutrients [79], rather than simple mass-balance processes. Our study also only focused on the fluxes between seawater and fresh water, but it is worth noting that *P. ordensis* also contribute to moving energy within those biomes. Despite the fact that juvenile growth appears to occur in seawater, adults might spawn and be preyed in the intertidal zone. Within the river, growth could be supported by terrestrial carbon [40] and be allocated in other reaches of the streams [54], or even return to terrestrial ecosystems via predation by birds. Therefore, although the study focused on fluxes across the freshwater-marine ecotone, it is worth noting that diadromous fish like *P. ordensis* may also transport biomass within and into other biomes.

4.3 Revisiting the role of diadromous fishes on the allocation of subsidies across the freshwater-marine ecotone

Contrary to expectations [18], our model predicted that fresh water may act as a sink of marine-derived biomass driven by a catadromous fish. Given the very high abundance of *P. ordensis* and other catadromous species, such as barramundi, *Lates calcarifer*, tarpon, *Megalops cyprioides*, and other mugilids across northern Australia, we extended our model to other life-history traits. The extension of the model shows that when considering skipped spawning, catadromous fishes are much more likely to act as a net biomass flux to fresh water. For instance, barramundi are characterized by relatively rapid growth [80], high ratio (>10) between mass at spawning and at freshwater entry, and relatively higher survival than *P. ordensis* based on telemetry and ageing [23]. Considering the

requirements of this species to migrate from freshwater to marine spawning grounds, one might predict that barramundi acts as a net export of energy to the sea. However, this species also shows a high variability of migratory strategies [81], including a high prevalence of skipped spawning [23], which our model suggest may invert the source-sink coupling between marine and freshwater ecosystems.

We expect that the predictions of our models may apply to other diadromous fishes. However, it is worth noting that our model only considers subsidies in the form of fish biomass and might not apply to specificities of other life histories [82]. Some fish, such as Atlantic salmon, consume most of their energy reserves (up to 70%) for long distance migration, maturation and sexual development [83]. By doing so, fish contribute subsidies in the form of excreted nutrients in the spawning habitat. For instance, anadromous shad lose ~30% of weight while migrating from the marine environment into rivers [84]. However, nutrients that are excreted in the growing habitat (e.g., energy reserve consumed by salmon in the ocean) do not contribute to biomass flux across the freshwater-marine ecotone as they represent turnover of autochthonous (i.e. formed where it is found) organic matter.

While our model contains several simplifications, we believe it has potential utility as a framework in many cases to examine the allocation of biomass by diadromous fishes. For example, iteroparous Atlantic salmon (*Salmo salar*) are usually considered as transporters of energy and nutrients to streams [85,86]. However, they also show high variability in reproductive strategy [87], with some populations composed of only ~5% repetitive spawners [88]. Thus, despite the high ratio of adult:juvenile mass, we suspect that iteroparous anadromous salmonids, such as Atlantic salmon, could in some instances act as an export of energy to the sea in populations where when skipped spawning is common. This prediction is in line with historical estimates showing that even semelparous Pacific salmon (*Oncorhynchus* spp.) could act as a net flux of nutrients to the sea when the proportion of returners is low [89].

This inversion of nutrient flux was also explained by a nonlinear relationship between spawner abundance and the number of migrating smolts [90], illustrating that density dependence processes may drive feed-backs between fish life-history (e.g. the proportion of spawners) and biomass fluxes. In addition, while the direction of subsidies is determined by individual life history, the magnitude also depends on population dynamics. Increased skipped spawning by *P. ordensis* results in retention of biomass in fresh water, but could also decrease the total

amount of subsidies over the long term, as fewer individuals spawn, resulting in lower biomass flux of juveniles. In turn, skipped spawning is a conditional strategy in fish [22,24] that is strongly affected by environmental conditions. More studies are needed to integrate the relationship between the import and export of biomass in dynamic systems, and the implications for subsidy stability with regards to environmental variation.

5 Conclusion

The model derived in this study offers a simple tool to examine subsidy allocation across the freshwater-marine ecotone by diadromous fishes. We show that skipped spawning in a catadromous fish can lead to a net import of subsidies in freshwater ecosystems. Furthermore, we highlight that variation in migratory behaviour in other diadromous fishes could affect the source-sink coupling between the ocean and inland waters. Fish migration behaviours are affected by recent human disturbances, such as artificial barriers [91], global warming [92] and fishing pressure [93]. The tropical river systems of Australia's north are not exempt from environmental threats and our study highlights that conservation effort should be directed towards protecting connectivity between rivers and the sea to preserve the integrity of energetic fluxes across ecotone boundaries.

Author contribution

DC, MD and AK designed the study. DC, DB, AK and MD collected the data. GS and DC analysed the data. GS led the writing of the manuscript with substantial input from DC. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data will be deposit on Harvard Dataverse upon acceptance.

Ethic approval

This research was conducted under Charles Darwin University Animal Ethics Committee permit A12023 and

Kakadu National Park research permits RK786, RK805 and RK862.

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