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Robin Faillettaz

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UNIVERSITÉ PIERRE ET MARIE CURIE - PARIS 6
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ESTIMATION DES CAPACITÉS COMPORTEMENTALES DES LARVES DE POISSONS ET LEURS IMPLICATIONS POUR LA PHASE LARVAIRE

Un cas d'étude d'espèces démersales de Méditerranée Nord-Occidentale

Thèse de doctorat d'Écologie Marine



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Laboratoire d'Océanographie de Villefranche-sur-Mer
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Photographie de couverture d'une larve de mérrou brun, *Epinephelus marginatus* (Lowe, 1834), collectée le 22 Août 2014 en Baie de Villefranche-sur-Mer, réalisée par **Aldine Amiel et Eric Roettinger**, photographes de l'association *Kahi Kai* : www.kahikai.com

À Roland, mon grand-père.

PUBLICATIONS

Publications dans des revues scientifiques

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Faillettaz, R., Durand, E., Paris, C.B., Koubbi, P., Irisson, J-O. Swimming speeds of Mediterranean Fish Larvae Nuance Hjort's Aberrant Drift Hypothesis. *Soumis à Progress in Oceanography*.

Faillettaz, R., Picheral, M., Luo, J., Guigand, C., Cowen R.K., Irisson, J-O. Imperfect Automatic Image Classification Successfully Describes Plankton Distribution Patterns. *Soumis à Methods in Oceanography*.

Faillettaz, R., Koubbi, P., Irisson, J-O. Temporal Patterns of Fish Larvae Settlement in the Bay of Villefranche-sur-Mer, Ligurian Sea (Northwestern Mediterranean Sea). *Soumis à Marine Progress Ecology Series*.

Conférences

Faillettaz, R., Irisson, J-O., 2013. Drivers of Temporal Variability Of Larval Fish Abundances in Villefranche Bay (NW Mediterranean Sea) Over a 7-Year Time Series (2006-2012). *Poster*. 36th Larval Fish Conference, Miami, USA.

Faillettaz, R., Luo, J., Guigand, C., Cowen, R.K., Irisson, J-O., 2014. Fine scale Distribution of Larval Fish and Zooplankton Over a Mesoscale Front Explored Through High Frequency Imaging. *Poster*. Ocean Science Meeting, Honolulu, EUA.

Faillettaz, R., Blandin, A., Durand, E., Paris, C.B., Irisson, J-O., 2015. Behaviour Versus Oceanic Currents During the Dispersal of Larval Fish In the Northwestern Mediterranean Sea. *Présentation orale*. ASLO Meeting, Granada, Espagne.

Irisson, J-O., **Faillettaz, R.**, Blandin, A., Durand, E., 2015. Mediterranean fish larvae: orienteering champions. *Présentation orale*. COLLOQUE DRIVER – SUBLIMO : Restauration Ecologique Des Nurseries Des Petits Fonds Côtiers De Méditerranée, Les Embiez, France.

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INTRODUCTION GÉNÉRALE

Dès la fin du 19^{ème} siècle, les fluctuations d'abondances des stocks de poissons ont attiré l'attention des pêcheurs et des scientifiques. Ces derniers ont mis en place le Conseil Permanent International pour l'Exploration de la Mer (CIEM) afin d'identifier les causes de cette variabilité. Alors que certaines années la biomasse de reproducteurs semblait importante, les débarquements des années suivantes étaient faibles. Il arrivait également que, sans raison apparente, des années prospères succédaient à des années de faibles abondances. En se basant sur l'historique des débarquements de Hareng Norvégien, Johan Hjort remarqua que l'extraordinaire *cohorte* (i.e. une population de poissons de même âge) de 1904 avait constitué la majorité des débarquements des années suivantes. Il coupla ses observations à des expériences de capture-marquage-recapture afin d'estimer la variabilité interannuelle du comportement migratoire des adultes. Il en conclut que les fluctuations des stocks ne s'expliquaient pas que par le retrait d'individus par la pêche ou par des changements de comportement migratoire. Dans son rapport de 1914, Hjort présenta ses résultats et hypothèses et introduisit la possible importance majeure des jeunes stades de vie pour le repeuplement des stocks de poissons (p. 204) :

Fish stocks fluctuate enormously

The cause of those fluctuations is to be found in the larval stage

"We must therefore look to the later stages of the eggs to find the conditions which determine the numbers of individuals in any year class. This again leads us to the question, at which stage of development the most critical period is to be sought. Nothing is known with certainty as to this; such data as are available, however, appear to indicate the very earliest larval and young fry stages as most important."

Nous devons donc chercher les conditions qui déterminent le nombre d'individus dans chaque classe d'âge parmi les stades postérieurs aux œufs. Cela soulève la question de l'existence d'une période critique au cours de ces stades de développement. Il est encore impossible de confirmer cela ; cependant, les données disponibles à ce jour suggèrent que les plus jeunes stades larvaires et autres jeunes stades seraient les plus importants.

Ses conclusions s'avèreront être les précurseurs du développement de l'écologie larvaire au cours du siècle suivant [2].

Fish is one of the main sources of proteins worldwide

Aujourd'hui, le poisson représente 17% des apports en protéines animales de la population mondiale et jusqu'à 50% dans certaines régions du globe [3]. Dans un contexte de changement climatique et de diminution de la disponibilité des ressources marines, il apparaît urgent de mieux comprendre les processus responsables de la dynamique des populations de poissons, dont la phase larvaire pélagique est sans équivoque un élément clé [4]. Parmi ces processus, le comportement des larves de poissons pourrait jouer un rôle primordial. En effet, les petits organismes millimétriques et transparents que sont les larves de poissons possèderaient des capacités comportementales remarquables. Cependant, l'éthologie des larves de poissons en est à ses prémices et, mis à part en milieu tropical, très peu de données empiriques sont disponibles.

Some fish larvae have surprisingly high behavioural abilities

La région de Villefranche-sur-Mer située dans la Mer Ligure, en Méditerranée Nord-Occidentale, a été choisie comme zone d'étude car l'interface entre l'environnement côtier et l'environnement pélagique y est très proche de la côte et donc facilement accessible. Comme nous le verrons dans ce travail, ce site est particulièrement adapté à l'étude des larves de poissons. Pourtant, ces dernières ont fait l'objet de peu de recherches dans la région. Par des expériences *in situ*, en laboratoire et de modélisation, cette thèse vise à collecter des données sur l'écologie des communautés de larves de poissons présentes dans les environnements côtier et pélagique de Mer Ligure. Tout au long de ce travail, il sera fait mention de la présence et de l'étendue des comportements des larves de Perciformes en milieu tempéré et, *in fine*, de l'importance potentielle de ces comportements sur la dispersion et la survie des larves de poissons.

ÉTAT DE L'ART

1.1 LE CYCLE DE VIE DES POISSONS DÉMERSAUX

La majorité des espèces de poissons *démersaux* (i.e. vivant à proximité du fond), qu'ils soient *benthiques* (i.e. vivant sur le fond) ou *benthopélagiques* (i.e. vivant entre le fond et le milieu pélagique), présente un cycle de vie comprenant une phase larvaire *pélagique* (i.e. vivant dans la colonne d'eau, sans interaction avec le fond) suivie d'une phase démersale (Figure 1.1). Les œufs peuvent être benthiques ou pélagiques et cette stratégie de ponte peut différer au sein d'une même famille. Dans un cas comme dans l'autre, les larves éclosent puis deviennent pélagiques. C'est donc dans le milieu pélagique qu'elles se développent jusqu'à devenir *compétentes* (i.e. prêtes à rejoindre un habitat d'installation) et doivent alors migrer depuis le large vers un habitat côtier. Après s'être installées dans un habitat favorable, les larves se métamorphosent en juvéniles, qui, à leur tour, deviennent matures et repeuplent ainsi la population d'adultes ; on parle alors de *recrutement* (i.e. l'arrivée de nouveaux individus dans une population [5]). Enfin, ces jeunes adultes se reproduisent, bouclant ainsi leur cycle biologique de reproduction.

Life history of demersal fishes is complex

Au début du 20^{ème} siècle, les travaux en écologie larvaire visaient avant tout à comprendre les fluctuations, l'objectif final étant de réussir à les prédire. La prédiction du recrutement est déterminante pour une bonne gestion des ressources marines exploitées [6], des populations au sein d'aires marines protégées [7], voire pour la combinaison des deux [8]. Aujourd'hui, les modèles d'évaluation de stocks sont de plus en plus complets et s'orientent vers une approche intégrée qui prend en compte l'ensemble des données biologiques disponibles [9], notamment les abondances des différents stades du cycle de vie des espèces. Les abondances des stocks d'adultes sont estimées à partir des débarquements réalisés et de l'effort de pêche fourni, tandis que celles des juvéniles et des stades *ichtyoplanctoniques* (i.e. œufs et larves de poissons) sont estimées lors de campagnes océanographiques (e.g. *l'International Bottom-Trawl Survey*, effectuée annuellement en Mer du Nord). Malgré les améliorations apportées par la prise en compte des abondances larvaires [10], il est encore extrêmement difficile, voire impossible, de prédire avec certitude les fluctuations des stocks de poissons exploités [11, 12] ou de l'arrivée de larves en phase d'instal-

Predicting fluctuations would help managing marine resources

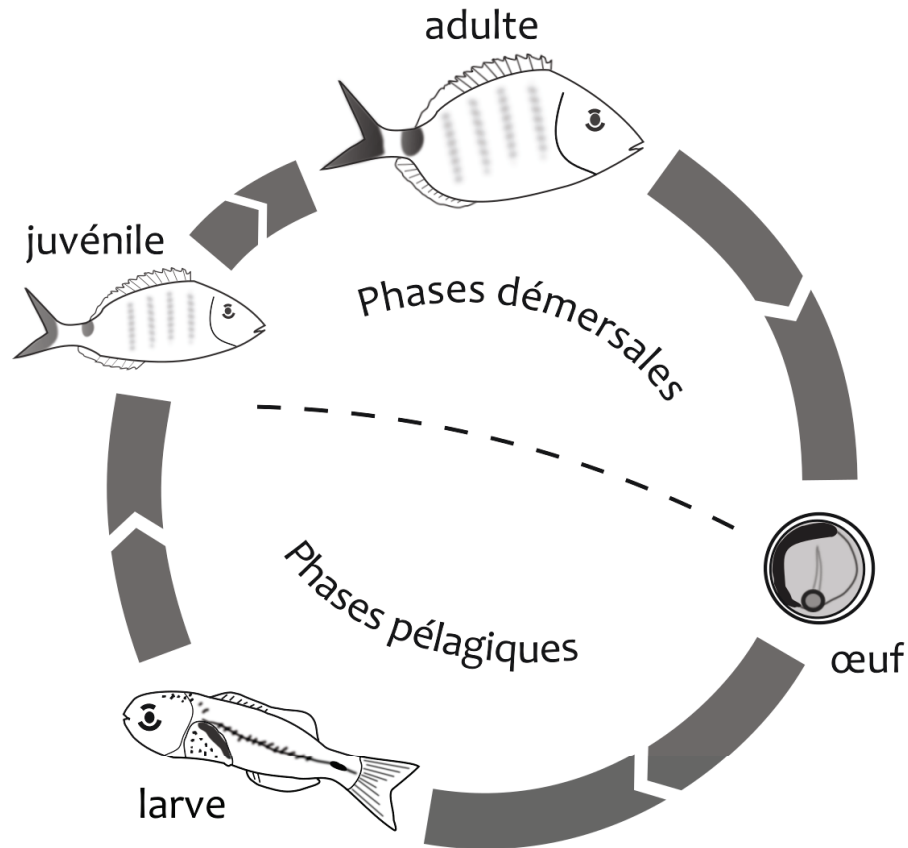


FIGURE 1.1 : Cycle de vie d'un sar (famille Sparidae), vivant dans un habitat côtier et pondant des œufs benthiques ou pélagiques.

lation d'une année sur l'autre [13]. Réussir à reproduire *a posteriori* des fluctuations observées reste exceptionnel [14].

Behaviour is one of many processes in larval fish ecology

La difficulté à prédire avec précision le recrutement d'espèces commerciales (ou l'installation d'espèces non-exploitées) est attribuable à la complexité des processus physiques et/ou biologiques en jeu au cours de la phase larvaire [15]. Le comportement des larves de poissons fait partie de ces processus.

Les capacités comportementales des larves de poissons augmentent progressivement jusqu'à la phase de transition de l'habitat pélagique vers l'habitat côtier [16] et joueraient un rôle essentiel pour la détection des habitats côtiers et la sélection du site d'installation [17]. Cependant, l'existence des différents comportements chez les jeunes stades larvaires, notamment les migrations verticales, suggère que ces capacités comportementales pourraient également avoir une influence tout au long de la phase pélagique. Cet état de l'art présente les principaux processus ayant lieu lors de la phase larvaire et permet de définir le contexte dans lequel s'inscrit le coeur de ce travail : le comportement des larves de poissons.

1.2 LES CONCEPTS FONDAMENTAUX DE L'ÉCOLOGIE LARVAIRE

Dès 1914, Hjort suggéra une possible influence de la condition des reproducteurs sur la qualité et la quantité des œufs produits, notamment à travers différents indices (contenus en graisses dans le foie, taille et poids des gonades), mais attribua une importance majeure aux taux de mortalité des jeunes stades larvaires [1]. La plupart des concepts actuels d'*écologie du recrutement* (i.e. l'étude des processus influençant le recrutement) sont basés au moins en partie sur les théories émises par Hjort : l'existence d'une période critique ("*Critical period hypothesis*" [1] p. 204-205) et l'influence de l'advection par les courants ("*Aberrant drift hypothesis*" [1] p. 206).

La première hypothèse a été l'objet du plus grand nombre d'études. Elle suppose qu'une des principales causes de la variabilité du recrutement serait le succès du premier nourrissage, c'est-à-dire la disponibilité des proies lors du passage d'une nourriture endogène, sur le sac vitellin, à une nourriture exogène sur des organismes planctoniques. Sur la base de ce concept et du cycle de vie des poissons, Harden Jones [18] estime que chaque stade (larvaire, juvénile et adulte) possède un habitat spatialement ou temporellement différent, leur permettant d'optimiser leur taux de survie. Cushing [19] a ensuite précisé le concept de période critique et de triangle de migration en suggérant que le pic d'abondance de larves de poissons devait être synchronisé avec les blooms de plancton ("*Match-mismatch hypothesis*"). Les larves subiraient donc une forte mortalité s'il existe un décalage temporel [19] ou spatial [20] entre les périodes d'abondance de larves, qui dépend de la reproduction des adultes, et de l'abondance de leurs proies (Figure 1.2).

The success of first-feeding may be essential

Fish larvae abundance may need to match prey availability

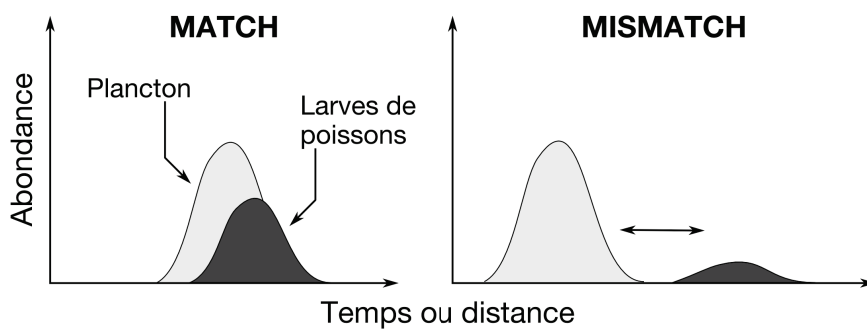


FIGURE 1.2 : Représentation du concept de "Match-mismatch". Ce concept suggère que si le pic d'abondance de larves de poissons n'est pas synchronisé avec le bloom de plancton, elles ne pourront pas se nourrir et la plupart mourront par inanition. Adapté de Cushing [19, 20].

*In upwelling systems,
calm periods
concentrate prey ...*

En se focalisant sur les zones d'upwelling hautement productives, Lasker [21] proposa le concept d'océan stable ("*Stable Ocean hypothesis*"), repris ensuite par Cury & Roy [22] qui suggèrent l'existence d'une fenêtre environnementale optimale ("*Optimal Environmental Window hypothesis*"). L'alternance entre périodes d'upwellings et périodes de calmes permettrait d'accumuler les proies des larves de poissons dans des couches fines de forte densité par des processus physiques, ce qui favoriserait leur nourrissage et par conséquent leur survie.

*... but mixing periods
may also be necessary*

Cependant, de trop longues périodes de calmes mèneraient à une limitation de la disponibilité en nourriture et des vents forts créeraient une turbulence excessive qui contrôlerait les pertes par advection et disperserait les patches de plancton, limitant également le nourrissage des larves de poissons par des processus physiques. En parallèle, plusieurs auteurs ont estimé que la mortalité larvaire n'était pas homogène au sein d'une même population et que les larves ayant une croissance plus lente avaient une probabilité de survie plus faible, amenant ainsi les concepts liés à l'importance de la durée des stades de vie ("*Stage-Duration hypothesis*" [23], "*Growth-Mortality hypothesis*" [24] et "*Bigger is Better hypothesis*" [25]).

*Larval size, growth rate
and pelagic duration
influence survival*

*Currents may transport
larvae away from
favourable areas*

La seconde hypothèse de Hjort [1] ("*Aberrant Drift hypothesis*") suggère que les larves de poissons sont transportées de façon passive par les courants et que celles dispersées loin de leur habitat d'installation subiraient une mortalité massive. En effet, il a observé que des larves de poissons, à des stades de développement parfois avancés, se trouvaient régulièrement éloignées de leur site de ponte. Il suggéra que ces larves pélagiques ne pourraient pas rejoindre un habitat d'installation avant de se métamorphoser en juvéniles. La morphologie de juvénile n'étant pas adaptée au milieu pélagique, ces larves seraient donc perdues. Cette hypothèse a généré moins d'études que celle de la période critique. Iles & Sinclair [26] et Sinclair [27] en ont toutefois repris la base pour définir le concept de rétention stable ("*Stable Retention hypothesis*" ou "*Membership-Vagrancy hypothesis*"). Il suggère que le facteur limitant du recrutement est la rétention physique des larves à proximité des *zones de nurseries* (i.e. leur habitat d'installation). Le comportement des adultes aurait donc un rôle important, notamment en sélectionnant des zones et périodes de pontes où les conditions océanographiques seront relativement stables et favoriseront la rétention des œufs et larves. Suivant l'hypothèse de "dérive aberrante", les larves sont considérées comme des organismes passifs et celles qui ne seraient pas retenues à proximité de leur zone de nurserie seraient donc perdues (Figure 1.3). Il est toutefois intéressant de noter que Hjort évoque, sans pouvoir le vérifier, que les capacités de

*Physical retention may
reduce aberrant drift*

locomotion des larves pourraient vraisemblablement influencer leur transport.

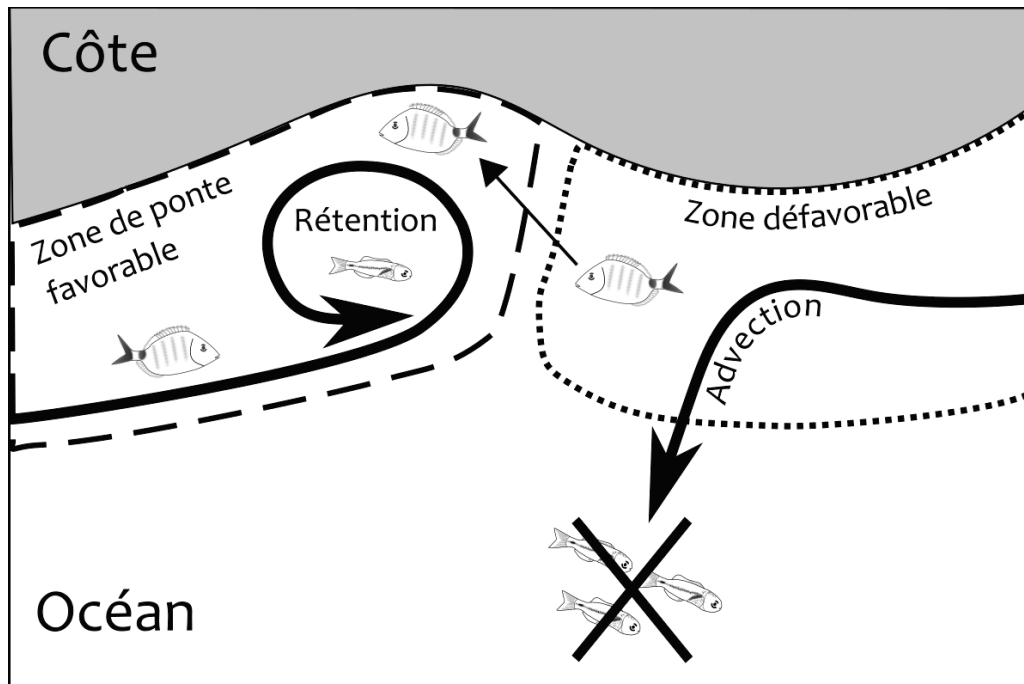


FIGURE 1.3 : Représentation des concepts de rétention stable et de dérive aberrante. Selon l'hypothèse de rétention stable, les adultes situés dans une zone de ponte défavorable (à droite sur le graphique) se déplaceront pour aller se reproduire dans une zone où les conditions favoriseront la rétention, par exemple dans un tourbillon permanent (à gauche sur le graphique). Selon les deux hypothèses, les larves qui ne seront pas retenues à proximité de ces habitats favorables seront transportées vers le large (en bas sur le graphique) et seront perdues.

Tous les concepts décrits ci-dessus ont été développés en se basant sur des observations en milieu tempéré, où la saisonnalité est marquée et les périodes de forte productivité sont limitées temporellement (e.g. en Mer du Nord, dans les systèmes d'upwellings de Humboldt, du Benguela ou de Californie). À l'inverse, la saisonnalité est moins nette en milieu tropical et la productivité des écosystèmes y est donc plus homogène au cours de l'année. De ce fait, les études sur l'écologie du recrutement en milieu tropical se sont focalisées sur l'importance des processus relatifs à l'installation des larves plutôt qu'à leur survie à la phase pélagique. Sale [28, 29] suggère que le flux d'installation des larves dans les habitats côtiers n'est pas homogène et dépend des conditions océanographiques, mais que ce sont les processus post-installation qui déterminent l'intensité du recrutement dans les populations adultes ("Lottery hypothesis"). La démographie

In tropical environments, oceanographic conditions determine larval supply rates ...

... and predation
determines recruitment
intensity

des populations en milieu tropical serait donc contrôlée par le transport des larves vers les zones d'installation, tandis que la mortalité serait essentiellement due à la prédation, à des niveaux déterminés par la densité des larves nouvellement installées [30].

La multiplicité des concepts exposés démontre la diversité des processus potentiellement déterminants pour le succès du recrutement. Considérant qu'ils sont susceptibles d'interagir les uns avec les autres, la *triade de Bakun* [31] reprend l'ensemble des concepts en définissant les trois conditions qui favorisent le recrutement : 1) l'enrichissement du milieu en nutriments ; 2) la concentration du zooplancton dans des zones propices au nourrissage ; 3) la rétention des larves de poissons par les processus océanographiques à proximité des zones de nurseries.

1.3 LES LARVES DE POISSONS DANS LE MILIEU PÉLAGIQUE

Nous avons vu dans la partie précédente que de nombreux facteurs sont susceptibles d'influencer la survie des larves à leur phase pélagique. De plus, les océans ne sont pas de grandes étendues homogènes, mais sont au contraire fortement structurés à toutes les échelles par des variables environnementales (saisons, conditions climatiques) et océanographiques (courants, distribution des masses d'eau) [32–34]. Ainsi, les conditions rencontrées par les larves de poissons seront extrêmement variables en fonction de leur distribution et de la période de l'année [35]. Dans cette partie, nous décrirons l'influence des structures océanographiques sur la distribution des larves de poissons et des conditions environnementales sur leur survie immédiate.

1.3.1 *Influence des structures océanographiques sur la distribution des larves de poissons*

Ocean structure is
reflected in hydrological
conditions

La structure spatiale des conditions océanographiques est un facteur majeur de la distribution des larves de poissons dans les océans, en particulier les fronts et les tourbillons [36]. Les fronts océaniques sont formés par la rencontre de masses d'eau de différentes densités, générant des zones de gradients horizontaux ou verticaux des propriétés physico-chimiques (température, salinité, nutriments, etc.) [37]. De manière générale, les zones frontales sont considérées comme des "hot-spots" de biodiversité [38, 39], puisque la production y est élevée et que les organismes passifs y sont concentrés par des mécanismes physiques [40], attirant ainsi des organismes de niveaux trophiques supérieurs (planctoniques [41] et/ou des poissons adultes [42, 43]). Les zones frontales de convergences (ou downwellings) favorisent

l'accumulation des larves de poissons et de leurs proies près de la surface [36]. Au contraire, les zones de divergences vont avoir tendance à les disperser, mais favoriseront la structuration spatiale des communautés de chaque côté du front [36, 44].

Les fronts marins peuvent être créés par des tourbillons (jusqu'à plusieurs dizaines de kilomètres de diamètre et 1000 m de profondeur), par des courants de marée (e.g. en Manche) ou encore par la topographie, communément entre le plateau continental et la pente (e.g. le front Catalan en Méditerranée Nord-Occidentale [45]). Ces fronts vont séparer spatialement différents assemblages de larves de poissons, qui coïncident généralement avec la distribution des adultes de part et d'autre du front (e.g. au Mexique : [46] ; en Mer de Chine : [47] ; Thaïlande [48] ; Australie : [49] ; Mer Méditerranée [50–54]). Par exemple, lorsqu'un front est localisé à la limite du plateau continental, les larves d'espèces côtières constitueront l'assemblage le plus proche de la côte, tandis que les espèces du plateau seront distribuées au-dessus de celui-ci. Les espèces océaniques (pélagiques et mésopélagiques) seront réparties de façon plus homogène entre le front et le large, mais peuvent également se retrouver concentrées au niveau du front. Ces limites spatiales entre les assemblages larvaires permettraient, entre autres, de les retenir à proximité de leur zone de ponte [31, 36, 44].

Fronts delimitate fish larvae distribution

1.3.2 *Influence des conditions environnementales sur la survie des larves de poissons*

Les fronts séparent donc différentes masses d'eau, qui auront des caractéristiques plus ou moins favorables à la survie des larves de poissons. En effet, une masse d'eau ayant une température élevée favorisera une croissance rapide des larves par rapport à une masse d'eau plus froide [55], augmentant ainsi leur probabilité de survie [23, 24]. De même, l'activité des larves est plus intense lorsque le taux d'oxygène dissous est élevé, ce qui favorisera la recherche de nourriture et aura également un effet positif sur la survie [56]. Les proies des larves de poissons ne sont pas distribuées de façon homogène [32] et, comme expliqué dans la partie précédente, leur disponibilité pourrait être un autre facteur pouvant influencer la survie larvaire [57, 58]. La présence de micro-turbulences permettrait d'augmenter le taux de rencontre avec les larves de poissons, même à de faibles concentrations [59]. À micro-échelle, les larves évoluant dans un environnement visqueux (avec des nombres de Reynolds faibles) pourraient avoir plus de mal à capturer leur proies par succion, jusqu'à les empêcher de se nourrir lorsque les concentrations de proies sont faibles [60]. *L'inanition* (i.e. le manque de nourriture) pourrait donc être un

Environmental conditions influence fish larvae survival

Many taxa predate on fish larvae

facteur de mortalité chez les larves de poissons. Il pourrait également l'être de façon indirecte puisque les larves en mauvaises conditions auraient plus de chance de se faire prédater [61]. La densité de prédateurs aura également une importance majeure, en particulier chez les plus jeunes stades [25, 41]. En effet, de nombreux taxa se nourrissent, en partie, de larves de poissons : principalement les poissons planctivores et le zooplancton gélatineux. On notera notamment que les éphyrules de *Pelagia noctiluca* sont capables de capturer des larves parfois plus longues qu'elles [62].

Description of fine scale distributions of fish larvae is needed

Pour des raisons méthodologiques, les taux de mortalité dus à la mortalité naturelle, à la prédation et à l'advection restent difficiles à mesurer *in situ* [63]. Cela pourrait en partie expliquer pourquoi la théorie de *Match-mismatch* n'a été que rarement vérifiée (sauf en Mer du Nord sur la morue [64] et l'Aiglefin [65, 66]) malgré les nombreux travaux qui l'ont testée [25]. Aussi, bien que les principaux facteurs de mortalité soient aujourd'hui identifiés, une description plus fine de la distribution des larves de poissons en relation avec leurs proies, leurs prédateurs et les conditions environnementales reste nécessaire à la compréhension des processus biologiques déterminants pour la survie des populations larvaires pendant leur phase pélagique [67, 68].

1.4 LA DISPERSION LARVAIRE

Dispersal is limited to the larval phase in many fish species

À l'échelle génétique, la dispersion permet de préserver la diversité, favorisant ainsi la résilience écologique [69]. À l'échelle écologique, la dispersion permet aux individus de se déplacer vers des zones plus favorables (meilleure disponibilité de nourriture, densité de prédateurs plus faible), ce qui augmentera leur probabilité de survie en cas de fluctuations du milieu, mais augmentera le risque de mortalité en cas de dispersion vers des zones défavorables [70]. Dans le cas des populations de poissons démersaux, les adultes peuvent être limités à des habitats fragmentés (e.g. les récifs coralliens) ou associés à certains habitats bien spécifiques (e.g. les estuaires ou les prairies de phanérogames comme la posidonie). Ainsi, il est fréquent que les adultes soient sédentaires et que les échanges entre les populations (i.e. la *connectivité*) soient limités à la dispersion de leurs propagules [71–74]. Au regard de la connectivité, une *population source* exporte des larves vers d'autres populations, tandis qu'une *population puits* en reçoit provenant de l'extérieur [75].

Pendant leur phase pélagique, les larves vont suivre un trajet dont le départ sera leur population d'origine. Toutefois, toutes ne vont pas survivre, atteindre un habitat d'installation et repeupler les populations. Il est donc important de différencier le *transport larvaire*, de la

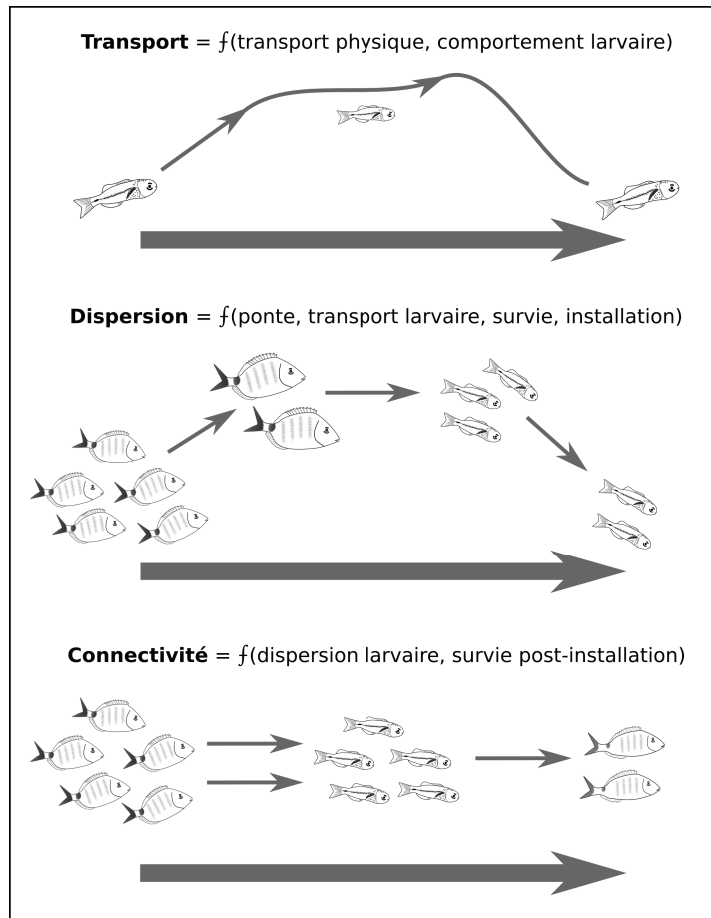


FIGURE 1.4 : **Transport larvaire, dispersion et connectivité.** Reproduit de [76].

dispersion et de la *connectivité* ([76]; Figure 1.4). Le transport larvaire correspond à la trajectoire suivie par une larve dans l'océan ; il est déterminé par l'advection par les courants et le comportement larvaire (qui sera discuté dans la section suivante). La dispersion représente l'export d'une larve depuis une population source vers une population puits ; elle dépend du transport larvaire et du succès d'installation dans un nouvel habitat. Lorsque des larves s'installent dans leur population d'origine (i.e. que la dispersion est nulle), on parle alors d'*autorecrutement*¹. La connectivité représente les connections *réalisées* entre les populations et dépend donc de la dispersion (ou de l'auto-recrutement) et de la survie post-installation ; lorsque le succès de la reproduction est également pris en compte, on parle de *connectivité reproductive* [76].

Larval behaviour influences dispersal

¹ Le recrutement n'a lieu que lorsque les larves entrent dans la population d'adultes, ainsi le terme autorecrutement est un abus de langage, puisqu'il s'agit en fait d'*autoinstallation*.

*Marine populations
were thought to be
open ...*

Les courants océanographiques peuvent transporter des organismes passifs sur plusieurs dizaines de kilomètres par jour. Ainsi, les populations marines ont longtemps été considérées ouvertes et la dispersion à large échelle comme étant la plus probable [77–79]. Les études empiriques sur la dispersion larvaire sont toutefois limitées puisque les larves de poissons sont difficiles à marquer et à suivre. Les études *in situ* se sont donc focalisées sur l'*autorecruitment*. De nombreuses méthodes ont été utilisées, notamment de génétique avec des analyses de paternité et de la variabilité des régions hypervariables de l'ADN [80, 81], de capture-marquage-recapture [82–84], de microchimie des otolithes [85, 86] et de modélisation avec des modèles biophysiques d'advection lagrangienne [87–89]. La plupart des études empiriques et théoriques ont montré que la proportion d'autorecruitment pouvait atteindre plus de 30%, suggérant que, malgré la présence d'une phase pélagique propice à la dispersion, une proportion non-négligeable des propagules émises participe au repeuplement de leur population d'origine [74, 76, 83, 84, 86, 90–93].

*... but self-recruitment
appears to be quite high*

La connectivité est donc un paramètre clé de la dynamique des populations de poissons [87], qu'il est également essentiel d'appréhender de façon réaliste afin de gérer au mieux les ressources marines [94–97].

1.5 LES CAPACITÉS COMPORTEMENTALES INSOUÇONNÉES DES LARVES DE POISSONS

*Fish larvae are not
passive ...*

Les larves de poissons étaient traditionnellement considérées comme passives, leur transport n'étant déterminé que par l'hydrodynamisme [78, 98, 99]. Cependant, suite à la synthèse exhaustive de Leis [100], il est dorénavant admis qu'au moment de l'installation, voire dès la post-flexion, les larves de poissons démersaux ne sont plus *planctoniques* (i.e. qui dérivent avec les courants) mais *nectoniques* (i.e. capables de lutter contre les courants).

*... they migrate
vertically ...*

Le comportement de migrations verticales est sans aucun doute le mieux décrit de tous les comportements observés, tant en nombre d'espèces qu'en diversité des environnements explorés (e.g. Mer du Nord : [101]; Alaska, USA : [102]; Australie : [103]; Brésil (fleuve) : [104]; Mer Méditerranée : [62, 105, 106]). Dès les plus jeunes stades, les larves sont effectivement capables d'effectuer des *migrations nyctémérales* (i.e. modifier leur distribution verticale entre le jour et la nuit), leur permettant de se déplacer la nuit vers les couches de surface où les proies sont plus concentrées [107–109] tout en évitant les prédateurs visuels [110]. De plus, la plupart des espèces effectuent des *migrations ontogéniques* (i.e. au cours de leur développement). Les jeunes stades sont généralement distribués proches de la surface, tan-

dis que les larves plus âgées s'étalent en profondeur au cours de leur développement [111].

En milieu tropical, la plupart des larves en phase d'installation d'espèces de poissons Perciformes sont capables de nager en continu sur plusieurs dizaines de kilomètres [112]. Les larves de certaines familles (Acanthuridae, Lutjanidae, Scorpidae) peuvent même dépasser 100 km en seulement quelques jours [113, 114]. Ainsi, les larves de Perciformes sont capables de maintenir des vitesses moyennes de 10 à 40 cm s⁻¹ (0.5 à 1.5 km h⁻¹) pendant plusieurs heures et sans se nourrir.

... and many are proficient swimmers

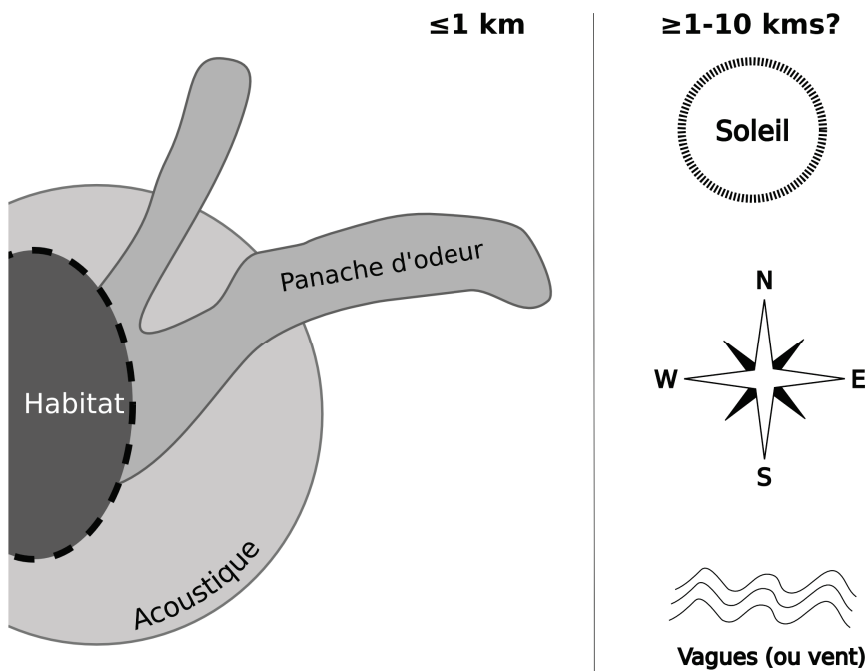


FIGURE 1.5 : Les différents processus suggérés permettant l'orientation des larves de poissons vers un habitat côtier. Adapté d'après [115].

Ces capacités de nage deviennent particulièrement pertinentes par le fait que plus de 60% des larves testées jusqu'à ce jour se sont montrées *directionnelles* (i.e. capables de nager dans une direction fixe [100]) et que les individus d'une même population *s'orientent* fréquemment dans une même direction [116]. Si les larves sont capables de détecter des habitats d'installation depuis le large, leur probabilité de les rejoindre avec succès devrait être largement augmentée. Toutefois, les mécanismes sous-jacents à l'orientation pendant la phase pélagique ne sont pas tous résolus. Le son a été régulièrement suggéré pour localiser l'habitat côtier, notamment grâce aux sons biotiques [117]. Cependant, des études récentes indiquent que l'orien-

Fish larvae can detect coastal habitats ...

tation par rapport aux signaux sonores n'est possible qu'à courte distance, probablement moins d'un kilomètre (Figure 1.5) [118, 119]. Les odeurs émises par les habitats peuvent permettre de les localiser à très courte distance (<10 m; Figure 1.5), en particulier les sites d'installation favorables [120]. D'autre part, les odeurs peuvent se répandre vers le large sous forme de panaches (e.g. les estuaires) sur de plus longues distances que le son (Figure 1.5) et les larves de poissons seraient capables de détecter leur présence [121, 122]. Cependant, pour s'orienter uniquement par rapport à l'intensité d'une odeur, les larves doivent être capables de se déplacer au sein du panache et de se souvenir des différences ressenties, ce qui semble peu réalisable. Ainsi, il a été suggéré que les larves de poissons pourraient utiliser les odeurs pour détecter la présence d'un habitat côtier, et auquel cas activer d'autres mécanismes d'orientation. Il est encore hypothétique que les larves de poissons soient capables de s'orienter lorsqu'aucun habitat côtier n'est détectable (Figure 1.5). Certains mécanismes d'orientation à longue distance ont été suggérés, comme le magnétisme ou la position des astres, mais n'ont pas été vérifiés *in situ* [100, 123, 124].

*... but can they orient
in the open ocean?*

En conclusion, les larves de poissons possèdent de formidables capacités comportementales, mais l'étendue de leurs capacités reste encore peu décrite et limitée à quelques espèces et environnements. De plus, la grande majorité des articles ayant traité du comportement de nage chez les larves de poissons juge de façon qualitative qu'elles ont le potentiel de fortement influencer leur dispersion, sans pour autant le tester quantitativement.

1.6 PRÉSENTATION DU TRAVAIL

Un certain nombre de thèmes de recherche ont été jugés comme insuffisamment explorés dans l'article de synthèse "*Emerging from Hjort's shadow*" du symposium NAFO-ICES-PICES sur l'écologie du recrutement (*trad. pers.* : "Il est temps de sortir de l'ombre de Hjort" ; [15]). Un point principal est le besoin de davantage d'études empiriques visant à tester la validité des concepts théoriques de l'écologie larvaire. En pratique, les différentes parties de cette thèse répondent à plusieurs des points soulevés comme étant critiques dans la synthèse évoquée ci-dessus, puis réaffirmés plus récemment [125, 126]. Le premier rappelle l'importance de comprendre l'intégralité du cycle de vie des poissons, en particulier des stades larvaires :

"Research and models on recruitment variability should broadly include all life stages. There is growing recognition that recruitment success can depend on variability in survival during all pre-recruit life stages."

La recherche et les modèles traitant de la variabilité du recrutement doivent inclure tous les stades du cycle de vie. Il est de plus en plus reconnu que le succès du recrutement dépend en partie de la variabilité de la survie durant tous les stades antérieurs au recrutement.

Ce point s'applique à l'ensemble de ce travail. En effet, nous nous sommes focalisés sur une seule zone d'étude, la région de Villefranche-sur-Mer, en Mer Méditerranée Nord-Occidentale (décrite en détail dans les Chapitres 2 et 4), à partir de laquelle nous avons étudié d'une part la distribution des jeunes stades larvaires pendant leur phase pélagique et d'autre part les processus ayant lieu lors de la phase d'installation. **La problématique de cette thèse est d'évaluer les capacités comportementales des larves de poissons de Mer Méditerranée, afin d'estimer leurs implications pour la phase larvaire.** Le comportement larvaire est donc mis en avant dans chacune des parties de ce travail.

La première partie de la thèse s'intéresse à la période pélagique de la phase larvaire. Le Chapitre 2 décrit la distribution horizontale et verticale des jeunes stades larvaires, principalement les stades de pré-flexion et flexion, à travers un front hydrologique. Ce chapitre est focalisé sur la distribution des populations de larves d'espèces démersales ainsi que sur leur comportement de migration nycthémerale. À l'aide d'imagerie *in situ* à haute fréquence, nous explorons également la distribution des larves de poissons à microéchelle (<1 m) en relation avec la distribution de leurs proies et prédateurs potentiels.

Fields studies are still needed to test theoretical concepts

Objective: estimate larval fish behaviour and its implication for the larval phase

Chap 2. Explore the offshore distribution of fish larvae during the pelagic phase

3. *Propose an automatic method to process planktonic prey and predators of fish larvae*

L'utilisation de méthode d'imagerie à haute fréquence est actuellement limitée par le traitement des grandes quantités de données générées [127]. Dans le Chapitre 3, nous proposons une méthode d'optimisation de classification d'images qui permet de passer à un traitement complètement automatique. Cette méthode facilitera le traitement des gros jeux de données collectés avec des méthodes d'imagerie, qui sont les plus adaptées pour étudier, *in situ*, la distribution d'organismes planctoniques à microéchelle (<10 m).

La seconde partie de la thèse s'intéresse à la phase d'installation qui a lieu à la fin de la phase pélagique. Cette partie s'intéresse donc à des stades larvaires plus avancés que la partie précédente, puisque toutes les larves sont alors au stade de post-flexion précédent la métamorphose. Elle est divisée en trois chapitres et répond à trois points supplémentaires soulevés par la synthèse évoquée ci-dessus, à commencer par le besoin de plus de séries temporelles :

"Long time series are essential to define conditions that control and regulate recruitment. Except for a few economically and ecologically important stocks [...], there are few observational time series that span decades to identify and analyze trends in abundance and recruitment variability, and to link variability to environmental factors."

Des séries temporelles sont essentielles afin de définir les conditions qui contrôlent et régulent le recrutement. Mis à part quelques stocks ayant une importance économique et écologique [...], il en existe peu qui s'étendent sur des décennies et permettent d'identifier et d'analyser les tendances de la variabilité d'abondance et de recrutement, mais également de mettre en relation la variabilité des conditions environnementales.

4. *Start a time series monitoring fish larvae settlement*

Ce travail a permis de mettre en place un suivi hebdomadaire et pluriannuel de l'abondance de larves en phase d'installation. Le suivi est effectué en synchronie avec les prélèvements hydrobiologiques effectués par l'Observatoire d'Océanographie de Villefranche-sur-Mer, en cours depuis plusieurs décennies (hydrologie, phytoplancton et zooplancton). Les données obtenues lors des trois premières années d'échantillonnage sont présentées dans le Chapitre 4.

Par ailleurs, le comportement larvaire reçoit une attention croissante, mais reste peu décrit, comme le souligne ce troisième point :

"Behavior and cues that trigger it in early-life stages are poorly known. Behavior plays a key role in many aspects

of early-life biology and dynamics [...] but often is insufficient or lacking in recruitment research. Incorporating behavior into models of early-life dynamics and recruitment processes is a particular need.”

Les comportements et signaux auxquels répondent les larves de poissons sont peu connus. Le comportement joue un rôle clé sur de nombreux aspects de la biologie et dynamique des stades larvaires, mais n'est pas suffisamment pris en compte dans l'étude du recrutement. Une des priorités est d'incorporer le comportement dans des modèles de dynamique larvaire et d'autres processus liés au recrutement.

Dans le but d'acquérir des données empiriques du comportement des larves de poissons en Mer Méditerranée, nous déterminons, *in situ*, les capacités d'orientation des larves de plusieurs espèces de poissons méditerranéens [Chapitre 5]. Nous démontrons la présence d'un mécanisme d'orientation à large échelle. Dans le Chapitre 6, nous présentons leur vitesse de nage. Le comportement des larves de poissons a probablement une forte influence sur leur transport, mais l'étendue de cette influence a rarement été testée explicitement. Cela est rendu possible grâce aux modèles biophysiques :

5. Detect fish larvae orientation behaviour in the open ocean and ...

6. Measure their swimming speed

“The coupled biological and physical modelling approach has had notable success in helping to explain mechanisms that generate recruitment variability but much remains to be done [...]. Most models have been developed as explanatory or inferential tools and relatively few as tools to test hypotheses, although the biggest contribution to understanding recruitment variability ultimately may come from that approach.”

L'approche de modélisation biophysique a eu un succès notable pour l'explication des mécanismes responsables de la variabilité du recrutement, mais il reste encore beaucoup à faire. La majorité des modèles a été développée dans une optique explicative ou inférentielle, mais peu ont été utilisés pour tester des hypothèses, alors que cela pourrait très certainement être leur plus grande contribution.

Dans le but de tester explicitement l'influence sur le transport larvaire des comportements observés dans les parties précédentes, nous les avons implémentés dans un modèle biophysique d'advection lagrangienne utilisant les conditions océanographiques correspondant à

6. Estimate the impact of oriented swimming on Hjort's "aberrant drift" concept

leur période d'installation. Nous en inférons leur potentiel à rejoindre l'habitat côtier par leur propre locomotion.

7. Discuss the importance of behaviour throughout the larval phase

Pour finir, les principaux concepts de l'écologie du recrutement sont mis en perspective avec les différents comportements larvaires, afin de discuter de l'importance de leur prise en compte pour appréhender les processus en jeu au cours de la phase pélagique des larves de poissons démersaux.

Partie I

LA DISTRIBUTION DE L'ICHTYOPLANCTON
EN MER LIGURE

“From the observations as to temperature, however, and distribution of the pelagic organisms, we could not but conclude that the fluctuations in this current were of so great extent as to render them of the highest significance to the animal life.” **Hjort, 1914**

DRIVERS OF LARVAL FISH DISTRIBUTION AT MULTIPLE SCALE ACROSS A HYDROLOGICAL FRONT

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2.1 INTRODUCTION

2.1.1 *Scales of larval fish distribution in the oceans*

Over centimetre to kilometre scales, hydrodynamics, predator-prey interactions and behaviour strongly structure the patchy distributions of planktonic organisms in pelagic environments [32–34]. As presented in the introduction (Section 1.3.1, p. 30), at mesoscales (10–100 km) and submesoscales (<10 km), plankton and ichthyoplankton distributions are primarily determined by hydrological structures like fronts and eddies [37, 38, 128]. At mesoscale, fronts may retain fish larvae close to their spawning location [31, 36, 44] or segregate development stages, with young stages on one side and older stages on the other side of the front [129]. Convergent flows at frontal features increase primary production [130] and mechanically concentrate organisms, including fish larvae [36, 40]. These structures may also attract ichthyoplankton predators, from adults fishes [42, 43], to chaetognaths and gelatinous zooplankton (e.g. siphonophores, ctenophores and medusae [41]). Fronts are thus often considered as “hot spots” of marine life [38, 39, 131]. However, the influence of these structures may be counter-balanced by behaviour or other biotic processes. Indeed, the day and night distributions of plankton are strongly influenced by diel vertical migrations [132, 133]. At microscales (<1 m to 10 m), biotic interactions such as competition and predation are likely to generate vertical gradients in the distribution of zooplankton. For example, in the Gulf of Mexico, predator avoidance is thought to vertically separate copepods, phytoplankton thin layers and gelatinous

zooplankton predators [109]. Off the coast of Massachusetts, interactions between internal waves and foraging drives a temporary overlap between layers of high copepod concentration and ichthyoplankton [134]. Larval fish have higher behavioural abilities than the vast majority of zooplankton larval stages and may therefore be less subjected to hydrological forcings and, at the same time, react more efficiently to their environment [100].

2.1.2 *The challenge of sampling fish larvae*

Historically, zooplankton and ichthyoplankton distributions have been sampled with pumps and regular or stratified plankton nets (regular: WP2, Bongo; stratified: MOCNESS, BIONESS, Multinet). However, nets cannot resolve the fine and microscale processes at which biotic interactions occur, because they usually sample (and integrate) over at least 10 m vertically and much more horizontally. While pumps collect physical samples at high frequency, they are limited to surface layers.

In situ imaging systems were developed with the aim of sampling microscale processes in the plankton and accelerating data processing using efficient automatic classification techniques [127, 135]. Several imaging systems have emerged, tackling different ecological questions by targeting different size spectra of organisms. The Video Plankton Recorder (VPR [136]) samples particles and zooplankton in the range [0.5 mm-5 mm], while the Underwater Vision Profiler (UVP [137]) images organisms from 1 millimetre up to few centimetres. The Shadow Image Particle Profiling Evaluation Recorder (SIPPER [138]) and, more recently, the *In Situ* Ichthyoplankton Imaging System, used for this study (ISIIS [139]), target large zooplankton up to several centimetres. ISIIS has been specifically designed to sample fish larvae that are patchy and rare [140]. Therefore, it samples larger volumes of water at a higher frequency compared to other methods (ISIIS: from 108 to 168 L s⁻¹; SIPPER 9.2 L s⁻¹; UVP: up to 20.0 L s⁻¹; VPR: 10 to 17 mL s⁻¹) and it has proved to be particularly adept at describing the fine-scale distribution of both ichthyoplankton [134, 141] and other taxa, including gelatinous zooplankton [128, 142].

2.1.3 *The Ligurian Sea and Liguro-Provençal current*

To study the influence of physical forcings and biological interactions on the distribution of fish larvae, we sampled a typical coastal jet: the Liguro-Provençal current, positioned on average 28 km from the shore, between the surface and 150-200 m depth, 25 km wide and

flowing at $25\text{--}35\text{ cm s}^{-1}$ towards the south-west [45, 143]. The current is present throughout the year and creates a marked, retrograde, hydrological front, with fresher waters on the coastal side and warmer, more saline waters offshore [144]. The frontal is located between the 38.2 and 38.3 isohalines [145]. Given the absence of continental shelf in the region, the Ligurian front is the main driver of plankton distributions in the region (phytoplankton: [146]; copepods: [145, 147]; sea urchin larvae: [148]). Coastal zooplankton species are more abundant in the peripheral zone (i.e. on the coastal side of the front). Indeed, the front may act as a barrier to dispersal [148], just like other Mediterranean fronts do [149]. It is also a nursery area to several copepod species [145]. In contrast, the central zone, which is located on the offshore side of the front, is characterised by low abundances of most zooplankton taxa.

The distribution of ichthyoplankton has never been described in the region. In the wider northwestern Mediterranean Sea, the distribution of fish larvae has been extensively described across the shelf-slope front off the Catalan coast. The Catalan front is created by the extension of the Liguro-Provençal current, which flows along the continental shelf that spreads over tens of kilometres from the shore. It displays high mesoscale variability and seasonality of both oceanographic conditions and larval fish distribution, but three to four main larval fish assemblages that correlate with bottom depth and/or front location have been systematically described [52, 53, 150–152]: shore-related species in the coastal zone, slope-dwelling species above the continental shelf and meso- and bathypelagic species mostly in the offshore side of the front.

The objective of this study is to provide a first description of the distribution of ichthyoplankton across a section of the Liguro-Provençal current in summer, in the Ligurian Sea, through the combination of high-frequency imaging and plankton nets samples. The working assumptions are that environmental factors would drive the meso- and submesoscale distribution of fish larvae (1 to 100 km scales), while fine-scale distribution would be determined by biotic interactions, between fish larvae and other taxa. We first describe the frontal structure and the distribution of fish larvae across that front, with a horizontal resolution of ~ 4 km; then we describe the vertical distribution of larval fish at microscale (< 1 m); and finally we relate the horizontal and vertical distributions of fish larvae to environmental variables and the distributions of potential prey, competitors and predators.

2.2 MATERIALS AND METHODS

2.2.1 *Sampling design*

Data were collected along a cross-front transect from Villefranche-sur-Mer towards the central zone of the Ligurian Sea, to fully sample the Liguro-Provençal current, in July 2013 (Figure 2.1).

Hydrological data were sampled on 4 successive transects: one sampled by a glider (July 19th to 22nd), another by the R/V Tethys II with a ship borne Conductivity Temperature Depth (CTD) sensor (July 19th) and two more by the *In Situ* Ichthyoplankton Imaging System (ISIIS; July 24th to 25th). The glider was equipped with a SBE41 CTD, acquiring hydrological variables (conductivity, temperature, fluorescence and oxygen) between surface and 500 m depth, with approximately one data point per metre depth and a horizontal resolution close to 1 km. A SBE911 was deployed from the ship at 9 stations (Figure 2.1 b), from 0 to 750 m. ISIIS was towed at 2 m s⁻¹ in a tow-yo fashion from the surface down to 100 m depth (Figure 2.1 c, d), for one night transect (from 22:00 to 05:00 local time) and one day transect (from 07:00 to 15:00 local time) with an average horizontal resolution of 1.7 km. It carried a fastCAT SBE49 CTD and a suite of environmental sensors that measured oxygen, fluorometry and photosynthetically active radiation (PAR) at a rate of 2 Hz (8 data points per m depth).

A ship borne Acoustic Doppler Current Profiler (ADCP) measured current speed between 4 m and about 160 m depth along the ship track.

Ichthyoplankton was collected at 19 stations by towing a Regent net (1 m diameter, 680 µm mesh size [153]) in oblique hauls at 1.5 m s⁻¹, between the surface and 100 m depth (Figure 2.1). Albeit at a limited number of stations, those samples allowed detailed taxonomic identification of fish larvae, most of which were early development stages (preflexion or flexion stages, both referred as *fish larvae* in the following). Most biological data were acquired in the form of *in situ* images, captured by ISIIS along the two (night and day) cross-front transects described above.

The *In Situ* Ichthyoplankton Imaging System (ISIIS; Figure 2.2) is a towed underwater imaging system [139] using backlighting shadowgraph imaging, which makes it ideally suited for small and often transparent planktonic organisms such as fish larvae. The version of ISIIS used here was slightly modified compared to [139]. It was equipped with a 2048 pixel line-scan camera scanning at 28 kHz (Dalsa Piranha 2 P2-22-02k40), hence producing a continuous image when towed at 2 m s⁻¹ (4 knots). It had a 10.5 cm field of view, a pixel

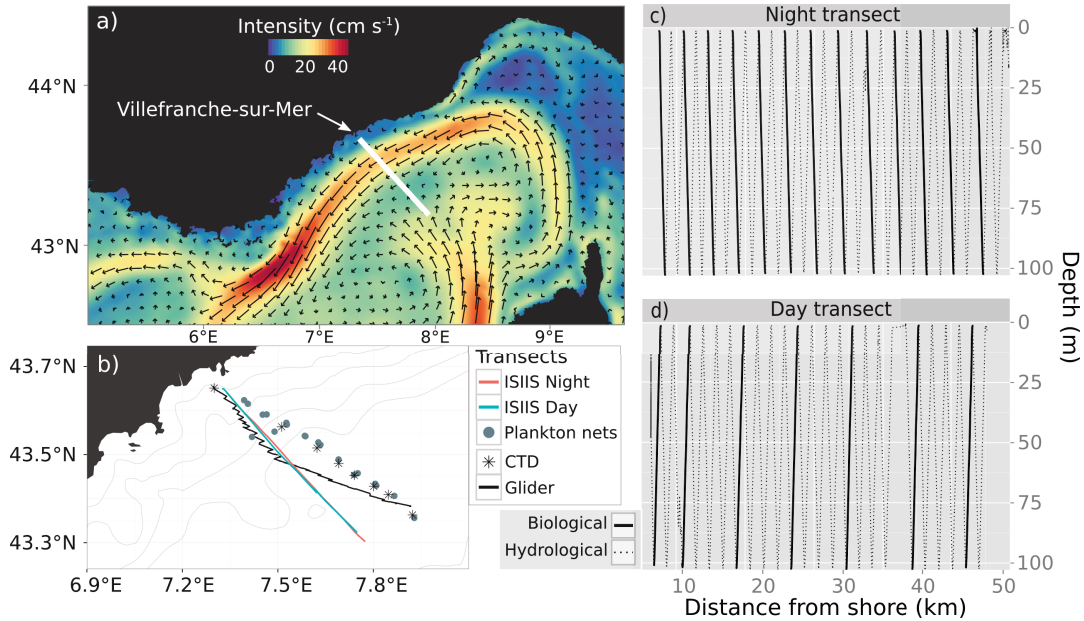


Figure 2.1: **a) Regional map with average current between the surface and 75 m during July 2013, computed from the 3h-time step outputs of the model MARS₃DMED.** The general shape of the Liguro-Provençal current is overlaid (grey arrows). The white line indicate the location of the cross-front section sampled in this study; **b) Detailed map of the location of the glider and ISiIS transects and the CTD and plankton nets stations.** **c) ISiIS casts sampled during the night transect and d) during the day transect.** All casts were used for the analysis of physical data. The casts considered for the analysis of biological data are highlighted (plain line).

size of 51 μm and a 50 cm depth of field. This configuration resulted in a sampling rate of 108 L s^{-1} . The system could resolve particles as small as 700 μm and up to tens of centimetres. This data provided fine-scale distribution of fish larvae and zooplankton (and associated environmental variables), but with poor taxonomic resolution. In addition, given the volume of data that ISiIS collects, not all casts could be processed and the horizontal resolution was 3.4 km for the night transect and 6.3 km for the day transect, on average (Figure 2.1).

2.2.2 Data processing

Physical data

The temperature and conductivity measurements of ISiIS and the glider were cross-calibrated with the ship borne SBE911 CTD system,

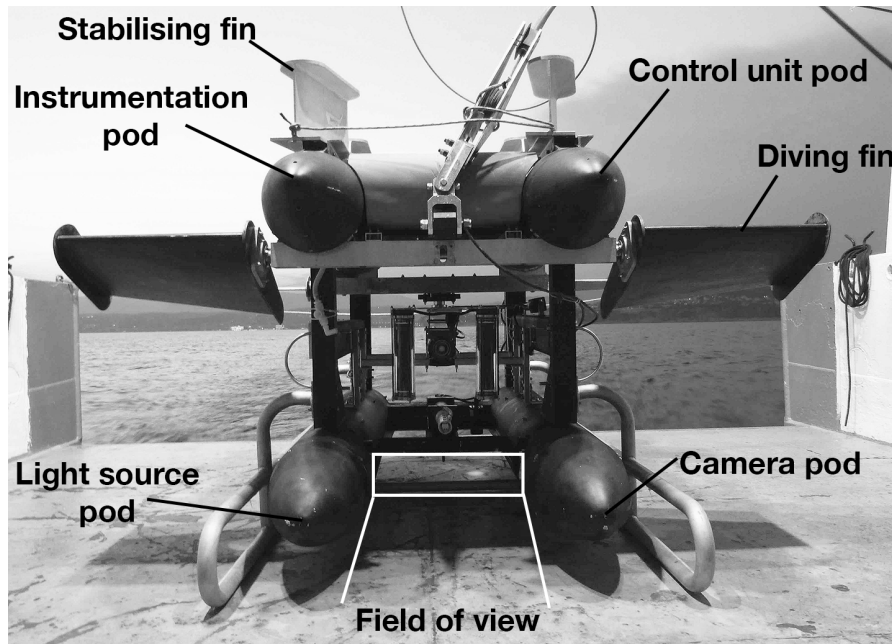


Figure 2.2: Frontal view of ISIIS. Its principal components are labelled.

which is annually calibrated to international standards. This allowed comparing values between instruments.

ADCP data provide the eastward and the northward components of the current over 4 m vertical bins, between 8 m down to a maximum of 246 m depth, by sending 43 (acoustic) *pings* every minute while the ship is moving. The depth reached by the pings depends on the abundance of reflectors in the water column (e.g. particles, zooplankton). During the cruise, the signal barely reached 160 m depth. ADCP data (here, a S-ADCP, RDInstruments BB 153.6 Hz) are usually processed by the “Service opérationnel SAVED” of the INSU www.dt.insu.cnrs.fr to clean and correct the raw flow velocity. In a regular situation, data are not filtered and display a noise close to 4 cm s^{-1} , which is due to within-bin variability of current and ship movement. However, the ship GPS connected to the ADCP was out of service during the cruise. The true bearing of the ship, i.e. the reference to define the measured flow direction, was thus not accessible. ADCP data were therefore processed with a non-standard method (a 5-pole Butterworth filtering that screened data based on 5-min bins instead of 1 min bins). This process resulted in a slightly higher noise ($\text{std}=7 \text{ cm s}^{-1}$), although data were well consistent throughout the transect.

Processing ichthyoplankton samples from nets

Plankton net samples were preserved in a 5% formaldehyde seawater solution buffered with sodium tetraborate at seawater pH right after collection. Each fish larvae was identified under a stereomicroscope to the lowest possible taxonomical level (species in most cases, but limited to genus or family for a few specimens) according to Lo Bianco [154], Richards [155], Fahay [156] and Lecaillon *et al.* [157]. The volume sampled was calculated from the distance travelled and the maximum depth of each haul. Abundances were standardised to concentrations of fish larvae per 1000 m³.

*Processing ichthyoplankton from ISIS images**Processing ISIS images*

ISIS collects a continuous stream of pixels, 2048 pixels in height. The stream was cut into square 2048 × 2048 pixels (4 megapixels) frames for practicality (example in Figure 3). Because the camera was continuously scanning the same line, a single speckle or scratch along the optical path created a continuous streak in the resulting 2D image. These streaks were removed by dividing each frame by the average of the previous 50 consecutive frames and normalising the result to [0, 255] in grey intensity (i.e. flatfielding).

The shadows of planktonic organisms or particles imaged by ISIS appear dark on a white background. A threshold was applied to each image to keep pixels with a below 195 grey level (darker than 24% grey) and regions exceeding 250 pixels in area were identified as objects of interest. Using *Zooprocess* [158], 46 features were measured on each object to characterise its transparency (five measures of grey levels: mean, mode, standard deviation, minimum, maximum), size and shape (length of the minor and major axes of the best fitting ellipse, Feret diameter, circularity, symmetry) and aspect (grey level histogram descriptors such as skewness, cumulative histograms, etc.).

Classification and identification of images

We used a computed-assisted classification procedure (*Zooprocess* and *Plankton Identifier* [158]) to ease the identification work. A machine-learning algorithm was trained to differentiate groups of interest based on the 46 measured features and a set of manually identified objects (learning set). Then, it proposed identifications for new objects, which were all validated by human operators. The learning set used for the classification was constructed through an iterative process, starting with images from the first cast and updated along the manual sorting. A total of 1.5 million objects were extracted, auto-

matically classified into 14 biotic and abiotic groups using a Random Forest classifier with 100 trees, bagging of 1, 6 features randomly selected per tree and leaf size of 2 objects. During manual validation, the identifications were refined into 46 groups (Table 2.1). All fish larvae were classified in a single group because it was not possible to identify them with confidence at a lower taxonomic level.

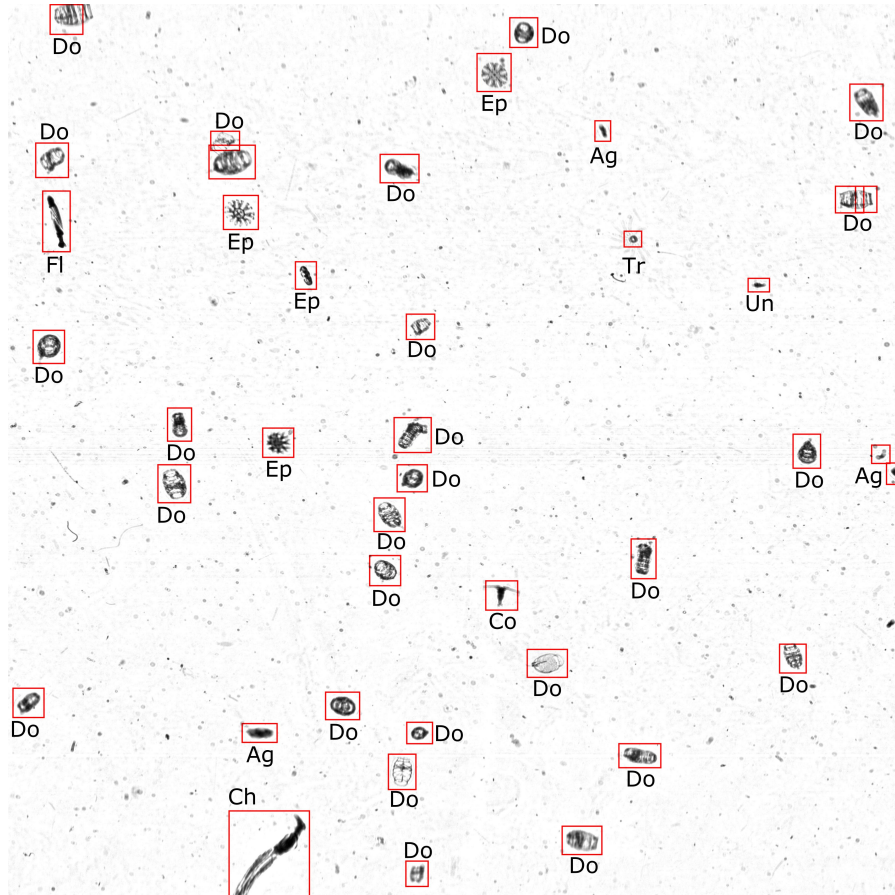


Figure 2.3: Example of a flatfielded 2048 x 2048 pixels frame collected by ISIIS. The bounding box of objects segmented and measured is drawn in red. All extracted objects are labelled (Ag: aggregates; Tr: Trachymedusae; Ch: chaetognath; Co: calanoid copepod; Do: doliolid; Ep: *Pelagia noctiluca* ephyrae; Fl: fish larva; Un: unidentified).

Table 2.1: **Prediction groups and refined groups used in the manual identification step** (O=Order, F=Family, G=Genus, G. sp=Genus species). Low abundance taxa were not included in prediction groups of the learning set because they were badly predicted.

Prediction groups	Validation groups
	Appendicularia F. Fritillaridae
	Appendicularia housing
fish_like	Appendicularia F. Oikopleuridae
	Other Appendicularia (mostly F. Kowaleskiidae)
	Objects out of focus
fish_like	Chaetognatha
	Amphipoda (e.g. G. <i>Phronima</i> spp or <i>Viblia</i> sp)
crust_copepods	Copepoda calanoids
crust_copepods	Copepoda F. <i>Calanidae</i>
crust_copepods	Copepoda G. sp <i>Euchaeta</i> marina
crust_copepods	Other Copepoda (e.g. G. <i>Oncaea</i> spp)
	Crustacean larvae
	Other crustaceans (e.g. Isopoda)
	Ctenophora tentaculated (F. Mertenziidae or G. <i>Pleurobrachia</i> spp or G. sp <i>Mnemiopsis leydi</i> cyddipids)
	Ctenophora F. Beroidae
det_aggregates	Marine snow
det_aggregates	Marine snow of dense particles (during the day only)
det_fibers	Thin fibres
doliolids	Thaliacean F. Doliolidae
	Medusae G. sp <i>Pelagia noctiluca</i> ephyrae
	Fish eggs
fish_like	Fish larvae
fish_like	Unidentified elongated organisms
jelly_trachy	Trachymedusae
	Narcomedusae G. <i>Solmissus</i> spp
	Narcomedusae G. sp <i>Solmundella bitentaculata</i>
	Other medusae (e.g. <i>Solmaris</i> spp or hydromedusae)
noise	Noise generated by water density anomalies
pelagia_tentacles	Tentacles of adult <i>Pelagia noctiluca</i>

(continued)

Table 2.1: (continued)

Prediction groups	Validation groups
phyto_diatom_chains	Phytoplankton G. <i>Trichodesmium</i> spp Phytoplankton diatoms chains Polychaeta
pteropods_other	Pteropoda Creseis-like
pteropods_other	Pteropoda Cavolina-like
pteropods_other	Other Pteropoda (e.g. <i>Cymbulia peronii</i>)
radiolarians_acantharia	Acantharia
radiolarians_colony	Radiolaria Colodaria in large colonies
radiolarians_solitarian	Radiolaria Colodaria solitary Other solitary Radiolaria
shrimps	Shrimps (e.g. Mysidaceae or Euphausi- acaee)
siphos_calycophore	Siphonophora F. Calycophorae Siphonophora F. Physonectae Unidentified objects

2.2.3 Data analysis

Physical data

To get a continuous picture of the environmental conditions across the various sections sampled, ADCP and CTD data were interpolated using linear interpolation over a 1.3 km × 1 m grid (distance from shore × depth), considering a vertical/horizontal anisotropy ratio of 1/1300 m, which was determined by comparing vertical and horizontal semi-variograms. The shallow layers of ADCP data (4 m and 8 m depth layers) were extremely noisy and removed prior to the interpolation. The isohaline lines 38.2 and 38.3, which delimitate the frontal zone [145], were used as a criteria to differentiate the peripheral (on the coastal side of the front), frontal and central hydrological zones and were represented on each graph.

Comparison between plankton nets and ISIIS

Larval fish concentrations collected with ISIIS were integrated over the water column for comparison with plankton nets hauls. Unlike ISIIS, plankton nets can become clogged when organism biomass is high. This might have diluted the concentrations when comparing the two methods, which were therefore standardised between 0 and 1 for each method, by dividing the concentration at each station by the maximum concentration observed along the transect.

Larval fish assemblages from plankton nets hauls

Larval fish species were categorised as coastal, benthopelagic, mesopelagic and pelagic using the Fishbase database [159]. The abundance of those groups were mapped across the cross-front transect. A Correspondence Analysis (CA) was performed to describe larval fish assemblages. Each station was associated with one of the three hydrological zones of the Ligurian front and the barycentre of each of those zones in the CA space was projected to help characterise the assemblage in each zone.

Vertical distribution of fish larvae collected with ISIIS

ISIIS provided the vertical position of each organism (later binned over 1 m depth bins) across a day and a night transect, thus allowing the exploration of diel vertical migration patterns. A modified version of the Kolmogorov-Smirnoff test that takes into account vertical patchiness [160] was used to test the difference in the vertical distribution of fish larvae between day and night. The distributions were also characterised by their barycentre (depth centre of mass, Z_{cm}) and its standard deviation (s_{cm}), computed as follows:

$$Z_{cm} = \sum_i \frac{c_i}{\sum c_i} Z_i$$

$$s_{cm} = \sqrt{\frac{\sum c_i (Z_i - Z_{cm})^2}{(n' - 1)(\sum c_i / n')}}}$$

where z_i is the middle depth bin i , c_i is a concentration of fish larvae in bin i and n' is the number of non-zero values of c_i (i.e. the number of bins with fish larvae; bins with no individual have a weight of zero).

Relationships between larval fish concentrations and hydrological conditions measured by ISIIS

Fish larvae concentrations and average hydrological conditions were computed in each 1 m depth bin along ISIIS' track. From these 1339 data points of the night transect and 721 from the day transect, Boosted Regression Trees (BRT [161]) were used to explore the relationship between larval fish concentration and environmental variables (temperature, salinity, oxygen concentration and fluorescence), separately for day and night. In this *physical BRT*, a Poisson distribution was assumed for fish larvae concentrations (in individuals per 1000 m³), interaction depth was set to 4, shrinkage to 0.001 and number of trees to 3995, based on 5-fold cross validation.

Relationships between fish larvae and other zooplankton from ISIIS images

In the same bins, the concentrations of other planktonic organisms seen by ISIIS were computed. A second BRT analysis related the residuals of the physical BRT described above to the concentrations of zooplankton taxa potentially interacting with fish larvae (Table 2.2). These residuals represented the information that was not explained by environmental factors and were thus driven by smaller-scale processes, which may be related to biological interactions. In this *biological BRT*, a Gaussian distribution was used because, unlike concentrations, residuals were not bound at 0. An interaction depth of 5 levels was selected, with shrinkage of 0.001 and number of tree to 4660, based on 5-fold cross validation.

Table 2.2: Taxa identified from ISIIS data which may interact with fish larvae.

Zooplankton taxa	prey	Competitors	Predators	References
Copepoda calanoids	Some	Some	Some	[162–164]
Crustacean larvae	YES	NO	NO	[162, 164]
Appendicularia Oikopleuridae	YES	NO	NO	[162, 165]
Chaetognatha	NO	YES	YES (ambush)	[166]
Medusae <i>Pelagia noctiluca ephyrae</i>	NO	YES	YES (tentacles)	[62, 167]
Trachymedusae	NO	YES	No	[F. Lombard, <i>pers. comm.</i>]
Siphonophora Calycophorae	NO	YES	YES (tentacles)	[168, 169]
Ctenophora tentaculated	NO	YES	Maybe (tentacles)	[170]

Diagnostic statistics for BRT models

For both physical and biological BRTs, the proportion of variance explained by the model was computed (R^2 equivalent), as well as the marginal influence of each hydrological and biological variable on larval fish concentration. Confidence intervals (90%, between the 5th and 95th percentiles) around the marginal effects were computed by bootstrapping the dataset 200 times for each model.

Boosted Regression Trees predict a response variable from all relevant explanatory and all their potential interactions, by construction [161]. However, to represent the relationship between one explain-

atory variable and the response variable, in a two-dimensional plot, the other variables are set to their mean values (i.e. the marginal influence). Interactions are therefore not visible on those plots even though they are considered in the model.

Data analysis tools

All data were processed with R (3.1.2) [171] with packages *plyr* (1.8.1) and *dplyr* (0.4.1) for data manipulation, *ggplot2* (1.0.1) for plotting, *akima* (0.5.11) for interpolation, *randomForest* (4.6.10) for image classification, *FactoMineR* (1.29) for the CA, *gbm* (2.1.1) for the BRTs, as well as custom code for the modified Kolmogorov-Smirnov test, the Z_{cm} and S_{cm} computation.

2.3 RESULTS

2.3.1 *Description of the frontal structure*

Hydrological structure

The hydrological structure of the Ligurian front during the study showcased a typical pattern, with a strong inshore-offshore gradient of increasing salinity and oblique isohalines (Figures 2.4 and 2.5). The transect conducted with the glider at the beginning of the cruise (Figure 2.4) showed that the frontal zone was deepest (120-150 m) and narrowest close to the shore, while it spread over approximately 10 km horizontally and between 70 m depth and the surface vertically (Figures 2.4 and 2.5). The general structure of the salinity gradient was persistent throughout the sampling period. Nevertheless, the current displayed intense meso- or submesoscale activity: the frontal zone moved ~10 km offshore during the five days of study. The limit between the peripheral zone and the frontal zone, at the surface, was at 17 km from the shore at the beginning of the study and at 28 km at the end; similarly, the limit between the frontal zone and the central zone moved from 26 to 36 km from the shore (Figures 2.4 and 2.5).

A sharp thermocline was present over the entire cross-front section throughout the sampling period, with temperature reaching 26°C in the surface mixed layer (down to 10 m) and dropping to 18°C at 25 m (Figures 2.4 and 2.5). In the upper 100 m, coastal waters were slightly warmer than offshore waters. Oxygen concentration was mostly stratified vertically, with highest levels in the upper 75 m of the water column (Figures 2.4 and 2.5).

Convection cells were evidenced by the downwelling of surface waters into two oblique plumes, visible in the salinity, oxygen and fluorescence data: one in the frontal zone at ~28 km from the shore

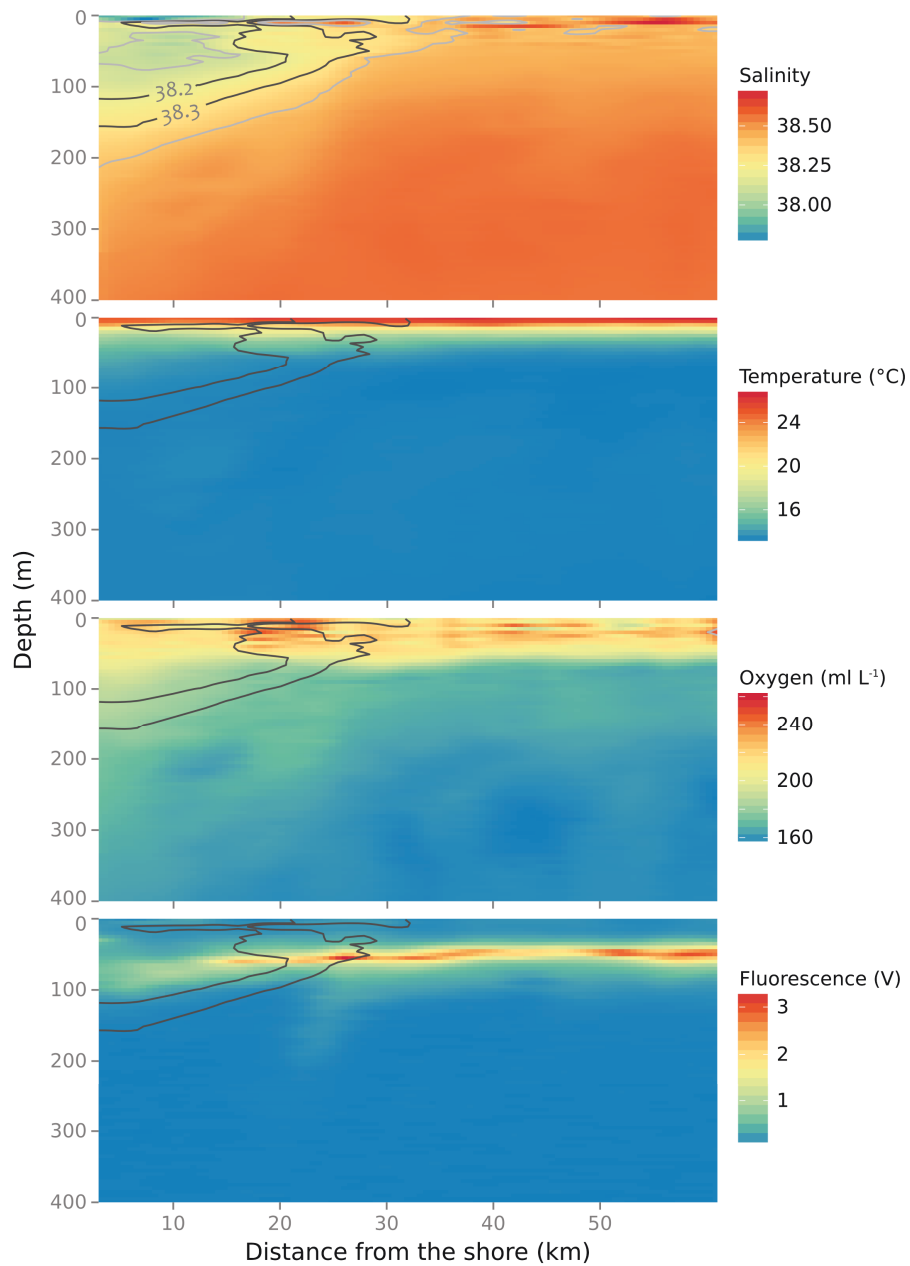


Figure 2.4: **Hydrological structure of the front, sampled with a glider between July 19th and July 22nd.** The 38.2 and 38.3 isohalines, which delineate the frontal zone, are overlaid on each graph (black lines).

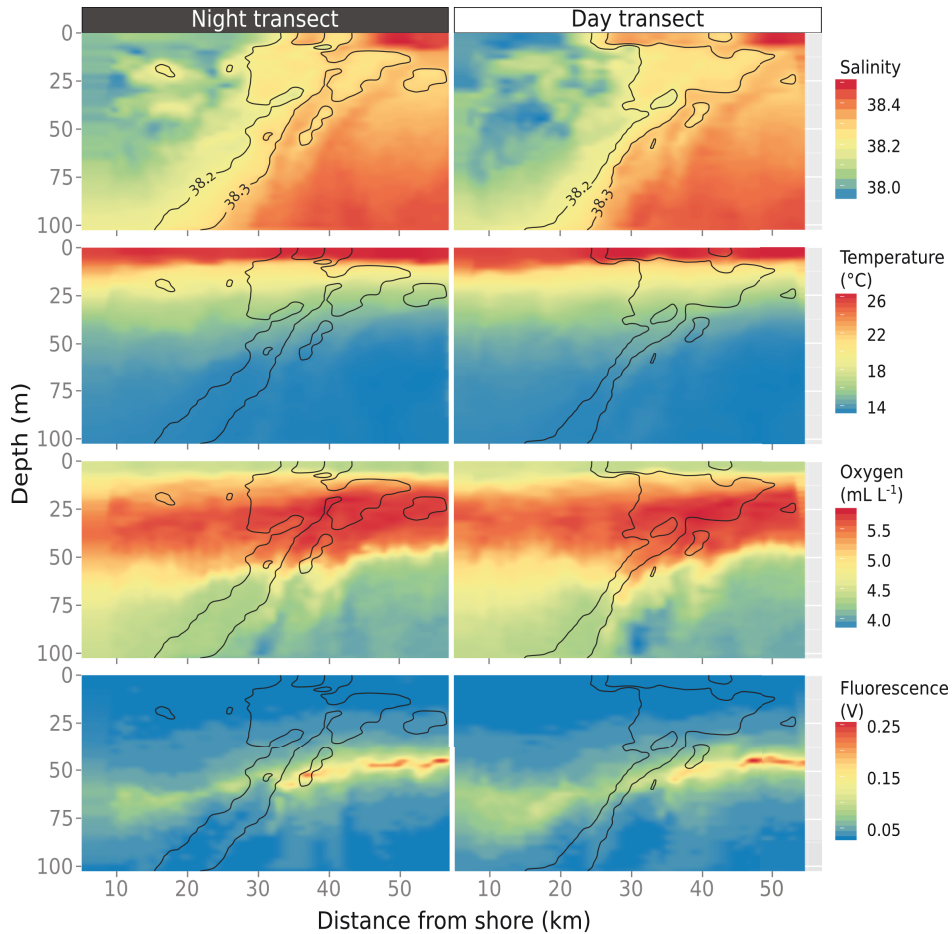


Figure 2.5: **Hydrological structure of the front during the two ISIIS transects, on July 24th and July 25th.** The 38.2 and 38.3 isohalines are overlaid on each graph (black lines).

(Figure 2.5) and another between the frontal and central zones (at 26 km from the shore on Figure 2.4 and 38 km on Figure 2.5), which led to fluorescence levels higher than average down to 200 m depth (Figure 2.4).

Fluorescence was maximum in the central zone and lower in the peripheral and frontal zones (Figures 2.4 and 2.5). The deep chlorophyll maximum was also shallower in the central zone (~50 m) than in the peripheral zone (~70 m).

Hydrographical structure

The structure of the current viewed through ADCP data matched the hydrological structure (Figure 2.6), with westward flow in the coastal zone, the core of the current between the peripheral and frontal zone and weak flow in the central zone. Current speed ranged from less than 10 cm s^{-1} up to 48 cm s^{-1} .

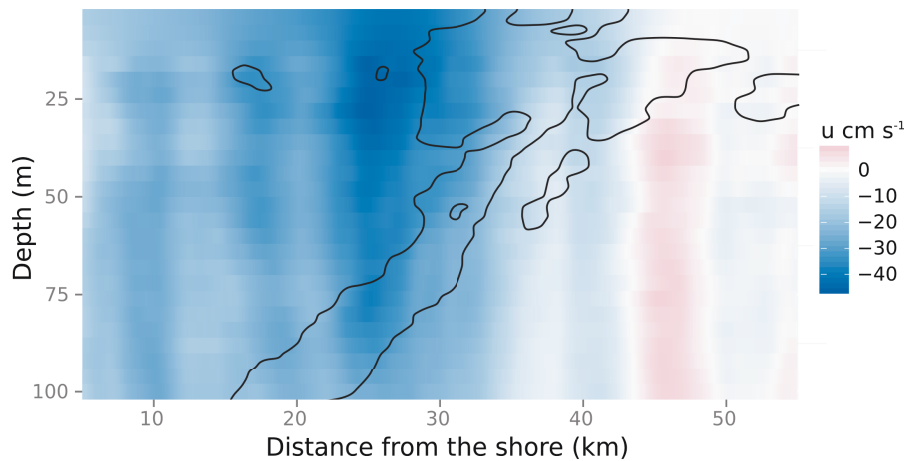


Figure 2.6: **Cross-front section of the major component of the current (u , eastward flow) obtained from ADCP measurements during the night transect.** The 38.2 and 38.3 isohalines delineate the frontal zone hydrologically (black lines).

2.3.2 *Ichthyoplankton community structure*

Cross-front distribution

A total of 671 fish larvae and 537 fish eggs were collected at the 19 plankton nets hauls, while 806 fish larvae were identified from the 20 ISIIS casts used for biological analyses.

With both ISIIS and plankton nets, concentrations of fish larvae integrated over the whole water column were higher within the first 25 km from the shore, that is to say in the peripheral zone, before the core of the current. Concentrations decreased drastically towards the central zone (Figure 2.7). Concentrations were not higher in the frontal zone as a whole. However, a patch of high concentration of *Auxis rochei rochei* (Risso, 1810) was observed around the distance between the frontal zone and the central zone, where the front reaches the surface and where larval fish concentration was also found to be higher with ISIIS data (Figure 2.7).

Similarly to fish larvae, fish eggs were collected in higher concentrations in the coastal and, to a lesser extent, frontal zones compared to the central zone (Figure 2.8). The station where many *A. rochei* were observed, at the limit between the frontal and central zones, also displayed high concentrations of fish eggs (6.0 per 1000 m³; Figure 2.8).

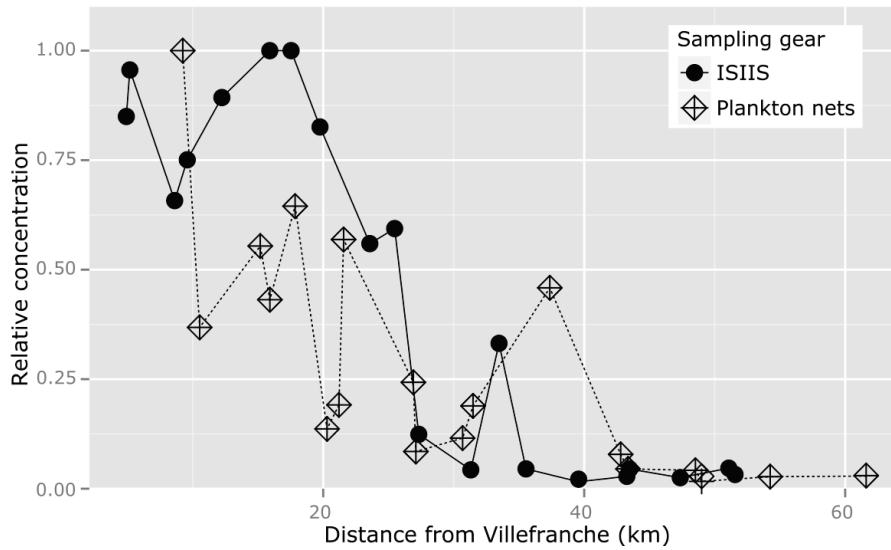


Figure 2.7: **Distribution of fish larvae across the Ligurian front, comparison between ISIIS and plankton nets.** Concentrations were standardised between 0 and 1 for each method.

Larval fish assemblages

Fish larvae collected with plankton nets belonged to 12 orders, 28 families and 46 taxa (Table 2.3). Most were preflexion or flexion stages, although some post-flexion were also collected.

Concentrations of larvae of coastal species were low in all hauls, ranging from 0 to 1.42 individuals per 1000 m³, but these species represented 41% of the total species richness (Table 2.3). Their distribution was restricted to the peripheral zone: not a single coastal fish larva was collected further than 26 km from the shore (Figure 2.9). Contrastingly, epipelagic species were less diverse (15% of the total number of species) but were the most abundant overall, reaching up to 9.32 larvae per 1000 m³. Epipelagic and mesopelagic species had similar distributions, being present on both sides of the front in concentrations ranging from 0.16 to 8.51 larvae per 1000 m³. Finally, benthopelagic species were the least common (4% of the total number of species) and least abundant (always <0.16 larvae per 1000 m³).

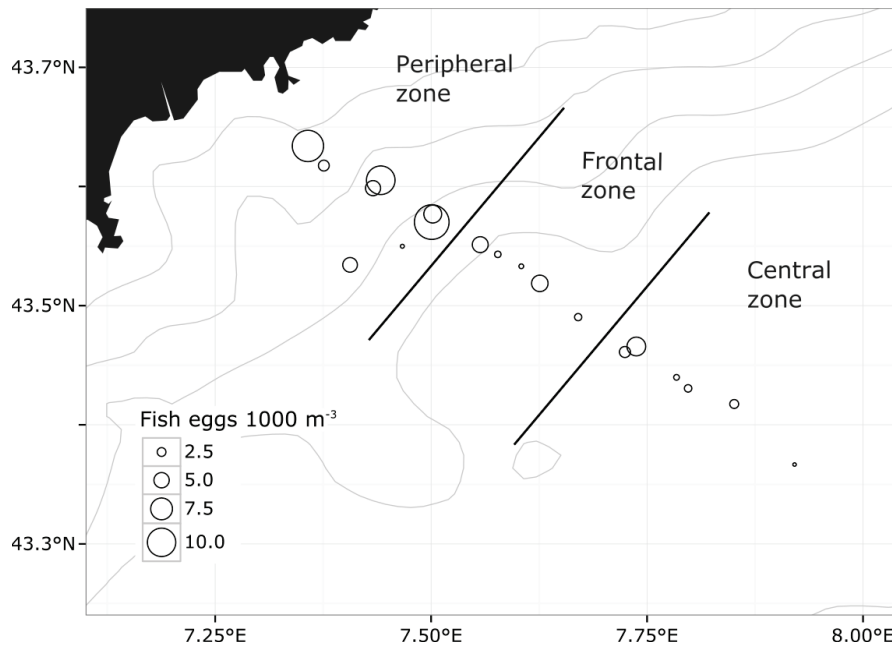


Figure 2.8: Distribution of fish eggs across the Ligurian front. The hydrological zones delineated in Section 2.3.1, p. 55 are reported here for reference.

Table 2.3: List of taxa collected with plankton net and their habitat as adults.

Species	Adult habitat
<i>Anthias anthias</i> (Linnaeus, 1758)	coastal
<i>Apogon imberbis</i> (Linnaeus, 1758)	coastal
<i>Arnoglossus kessleri</i> Schmidt, 1915	coastal
<i>Arnoglossus laterna</i> (Walbaum, 1792)	coastal
Blenniidae Rafinesque, 1810	coastal
<i>Callionymus</i> spp Linnaeus, 1758	coastal
<i>Cepola macrophthalmia</i> (Linnaeus, 1758)	coastal
<i>Chromis chromis</i> (Linnaeus, 1758)	coastal
<i>Coris julis</i> (Linnaeus, 1758)	coastal
Gobiesocidae Bleeker, 1859	coastal
Gobiidae Cuvier, 1816	coastal
<i>Lepidopus caudatus</i> (Euphrasen, 1788)	coastal
<i>Lepidotrigla cavillone</i> (Lacepède, 1801)	coastal
<i>Merluccius merluccius</i> (Linnaeus, 1758)	coastal
<i>Scorpaena</i> spp Linnaeus, 1758	coastal
<i>Serranus cabrilla</i> (Linnaeus, 1758)	coastal
<i>Serranus hepatus</i> (Linnaeus, 1758)	coastal

(continued)

Table 2.3: (continued)

Species	Adult habitat
<i>Sphyraena sphyraena</i> (Linnaeus, 1758)	coastal
Syngnathidae Bonaparte, 1831	coastal
<i>Auxis rochei rochei</i> (Risso, 1810)	epipelagic
<i>Engraulis encrasicolus</i> (Linnaeus, 1758)	epipelagic
<i>Sarda sarda</i> (Bloch, 1793)	epipelagic
<i>Sardinella aurita</i> Valenciennes, 1847	epipelagic
<i>Trachurus mediterraneus</i> (Steindachner, 1868)	epipelagic
<i>Trachurus</i> spp Rafinesque, 1810	epipelagic
<i>Trachurus trachurus</i> (Linnaeus, 1758)	epipelagic
<i>Glossanodon leioglossus</i> (Valenciennes, 1848)	benthopelagic
Macrouridae Bonaparte, 1831	benthopelagic
<i>Arctozenus risso</i> (Bonaparte, 1840)	mesopelagic
<i>Argyropelecus hemigymnus</i> Cocco, 1829	mesopelagic
<i>Benthoosema glaciale</i> (Reinhardt, 1837)	mesopelagic
<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	mesopelagic
<i>Cyclothone braueri</i> Goode & Bean, 1883	mesopelagic
<i>Cyclothone pigmaea</i> Jespersen & Tåning, 1926	mesopelagic
<i>Diaphus</i> spp Eigenmann & Eigenmann, 1890	mesopelagic
<i>Hygophum benoiti</i> (Cocco, 1838)	mesopelagic
<i>Lampanyctus crocodilus</i> (Risso, 1810)	mesopelagic
<i>Lestidiops jakayari pseudosphyraenoides</i> (Ege, 1918)	mesopelagic
<i>Lobianchia dofleini</i> (Zugmayer, 1911)	mesopelagic
<i>Maurolicus muelleri</i> (Gmelin, 1789)	mesopelagic
Myctophidae Gill, 1893	mesopelagic
<i>Myctophum punctatum</i> Rafinesque, 1810	mesopelagic
Paralepididae Bonaparte, 1835	mesopelagic
<i>Symbolophorus veranyi</i> (Moreau, 1888)	mesopelagic
<i>Vinciguerria attenuata</i> (Cocco, 1838)	mesopelagic

The correspondence analysis highlighted a main assemblage, strongly associated to the peripheral zone, which contained most species (Figure 2.10). Three species could be distinguished from the main assemblage: *Auxis rochei rochei*, which was associated to the central zone and *Arctozenus risso* and *Cyclothone pigmaea*, which were the two species most associated to the frontal zone. As already mentioned above, all coastal species were bound to the peripheral zone, just like the two bathypelagic species. Except *Auxis rochei rochei*, all pelagic species were also more associated to the peripheral zone than to the others. Indeed, they display the same decrease in abundance as coastal species, albeit less drastic, when moving offshore. Mesopelagic species

were spread between the peripheral and the frontal zones, but most were more associated to the peripheral zone.

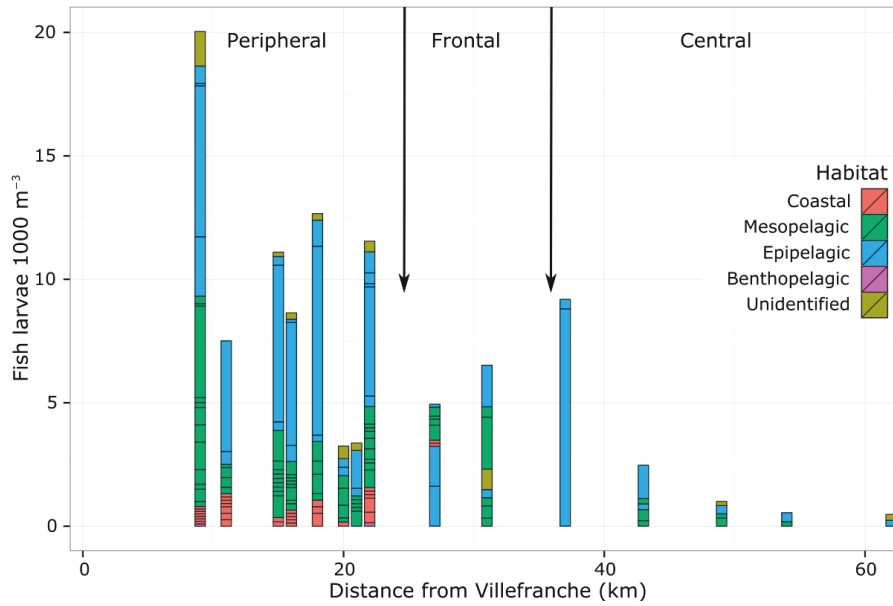


Figure 2.9: **Distribution of fish larvae taxa across the Ligurian front.** Bar height corresponds to the total concentration. Bars are stacked per taxon (horizontal lines). Colours represent the adult habitat of the species. The hydrological zones delineated in Section 2.3.1, p. 55 are reported here for reference.

Vertical distribution

ISIIS data highlighted that fish larvae were most concentrated in the upper 50m of the water column during both day and night, everywhere along the transect (Figure 11). More precisely, fish larvae were distributed with a main mode in the upper 5 m and a second mode between 10 m and 30 m depth at night ($Z_{cm}=13.4$ m) and in dense patches ($s_{cm}=4.2$ m, with up to 18.9 fish larvae per m^3). Very few fish larvae passed the 38.2 isohaline, especially at night, which confirms that most were limited to the peripheral zone. During the day, the depth barycentre shifted 22 m down ($Z_{cm}=35.4$ m, main mode around 20 m) and their distribution spread vertically ($s_{cm}=5.0$ m), but concentrations still reached 13.5 larvae m^{-3} in the peripheral zone, at 12 m depth. The vertical distributions of fish larvae, pooled over each transect, were significantly different between day and night (modified Solow K-S, $D=1.53$, $p < 0.01$; Figure 2.11).

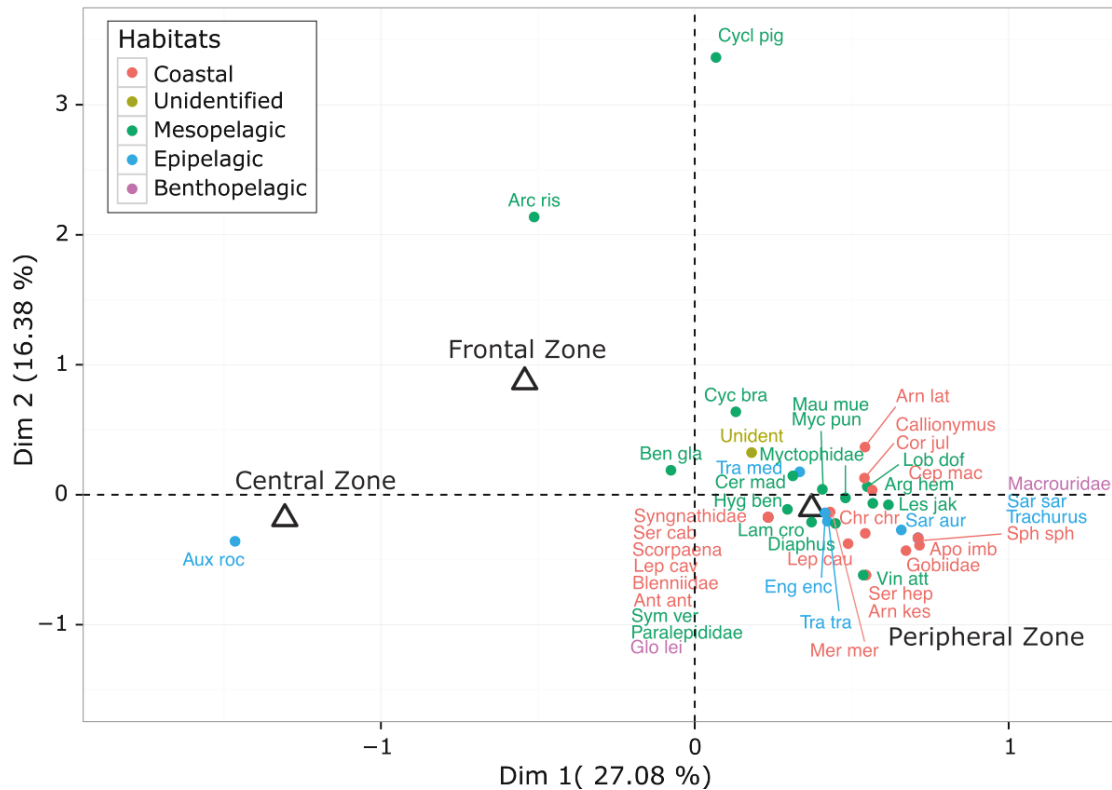


Figure 2.10: **Factorial plane of the correspondence analysis (CA) on the larval fish community sampled by plankton nets.** Hydrological zones are indicated as a qualitative supplementary variable (black triangles). Stations are not represented for clarity. Species located around a zone symbol tend to show larger relative abundance at station in this zone.

Relationships between larval fish concentrations and environmental variables

In Boosted Regression Trees models, environmental variables explained 71.0% of the variance in larval fish concentration in the night transect and 33.3% in the day transect. The models captured the main distribution patterns well, with highest larval fish concentrations in the coastal zone and above 30 m depth (Figure 2.12).

During both day and night, salinity was the main environmental variable affecting larval fish concentration (Figure 2.13). Fish larvae were more abundant at low salinity levels; their concentrations dropped passed 38.25. This showcases the influence of the front, which is most defined by salinity between 38.2 and 38.3, as already mentioned [145]. Temperature was the second most important variable at night (41.3%), with highest concentrations of fish larvae at high temperatures, i.e. near the surface (>25°C). A second mode of higher larval fish concentrations was observed between 16°C and 22°C, while colder

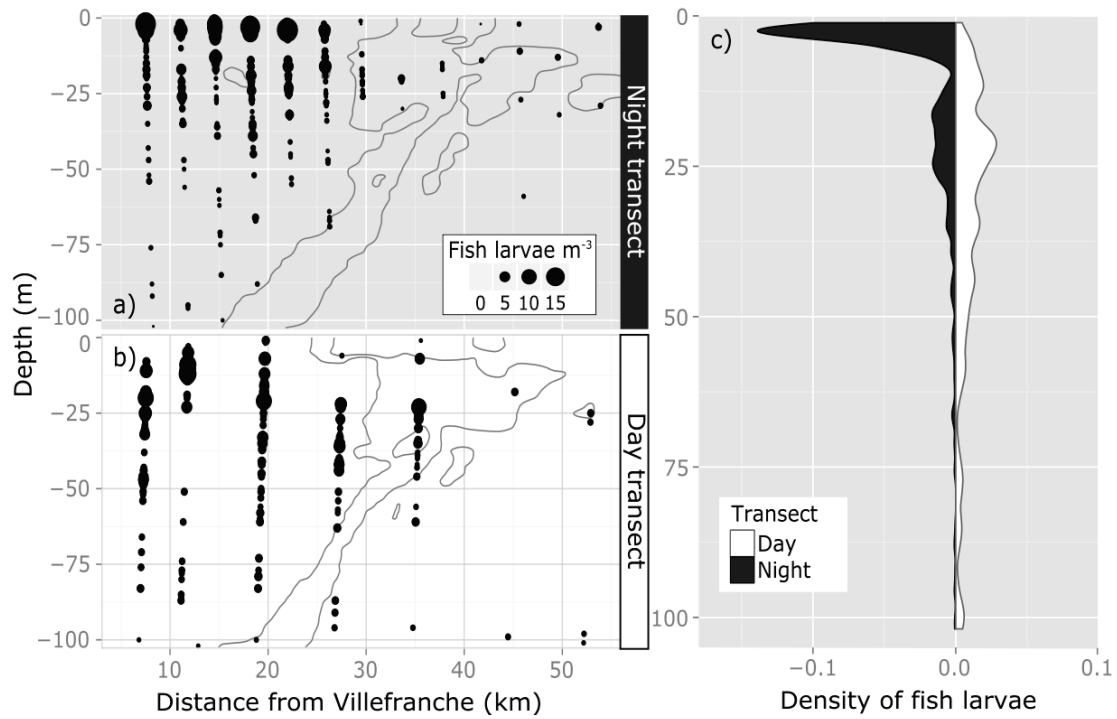


Figure 2.11: Distribution of fish larvae across the front seen by ISIIS during a) the night and b) day ISIIS transects. The 38.2 and 38.3 isohalines that identify the frontal zone are plotted for reference. c) Density of fish larvae along the vertical during the night and the day. Density was estimated through a Gaussian kernel method using a standard deviation of 0.8 m.

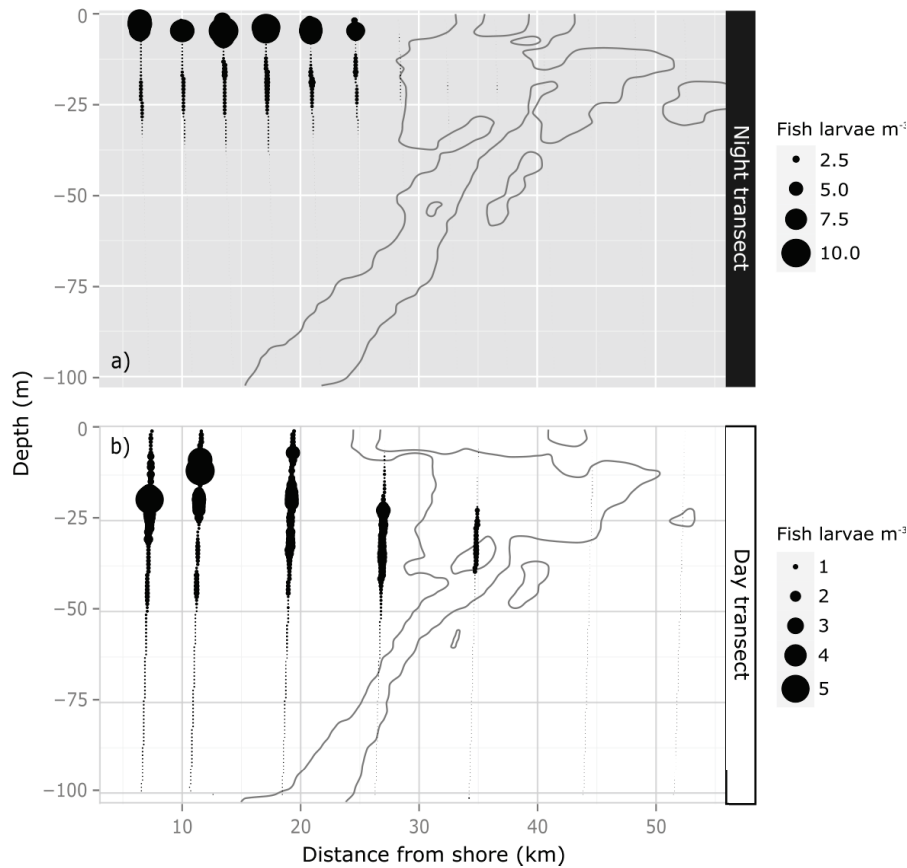


Figure 2.12: Predictions of larval fish concentrations using environmental variables in BRT models, for a) the night and b) day ISIIS transects.

temperatures were unfavourable (Figure 2.13). Temperature had less influence during the day (19.9%), with fish larvae being present at all temperatures, yet in lower concentrations in colder waters and maximum concentration around 17°C. Oxygen had more influence during the day (21.5%) than during the night (8.7%), with fish larvae favouring high oxygen concentration zones (Figure 2.13). Finally, fluorescence had almost no effect at night (3.2%). During the day, it had a slightly stronger influence (15.5% of the explained variance), with higher larval fish concentration observed between 0.05 and 0.075 volts, i.e. for quite low fluorescence values (Figure 2.13).

Relationships between larval fish and zooplankton distributions

Compared to physical BRT models, the biological BRTs explained a comparable proportion of variance at night (66.1% of variance explained) and a twice as much variance during the day (60.4%). At night, concentrations of trachymedusae, chaetognatha and *Pelagia noc-*

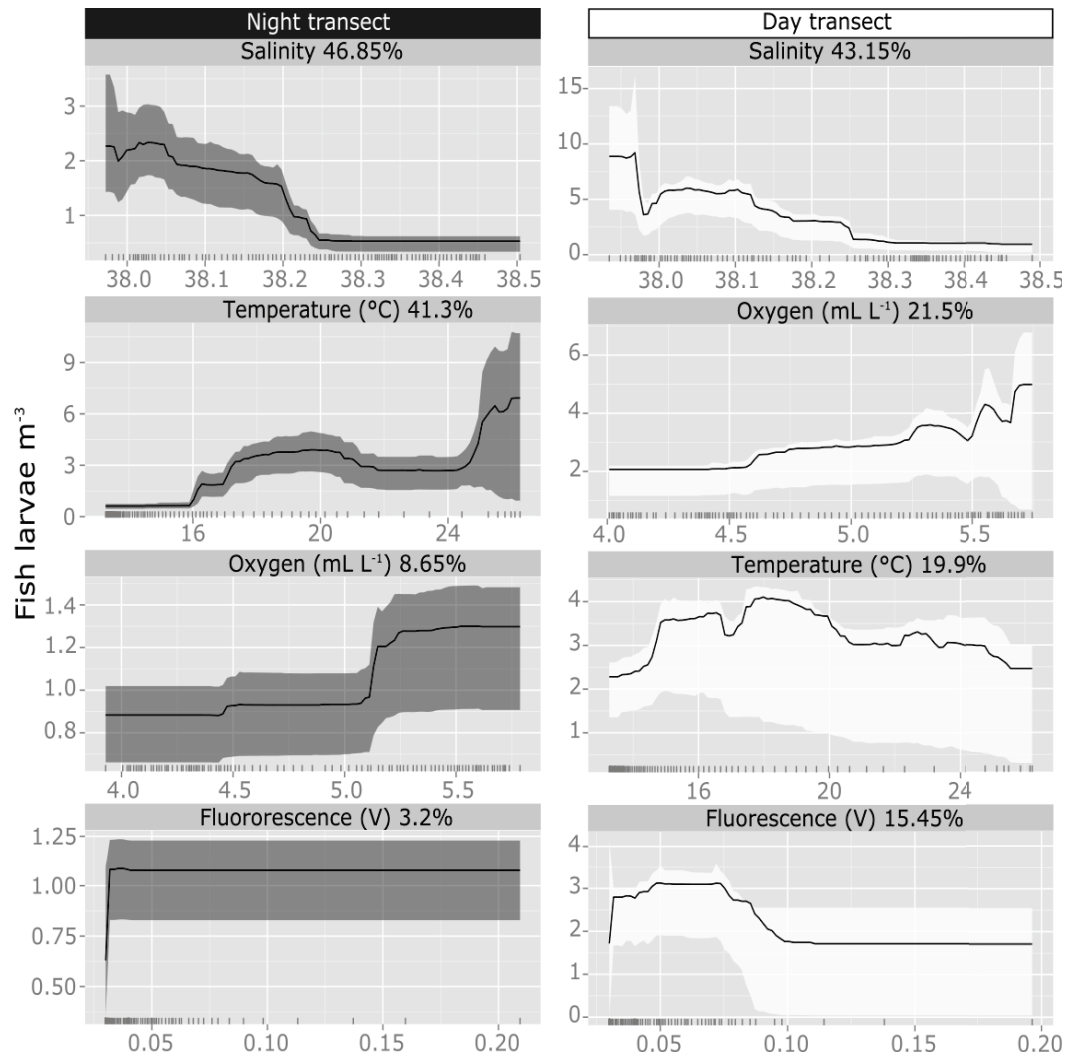


Figure 2.13: Marginal effects of environmental variables on larval fish concentrations (*physical BRT*) for the night transect (in grey; left panels) and the day transect (in white; right panels).

tiluca ephyrae explained 81.5% of these 66% variance (52.3%, 17.0% and 11.6% respectively; Figure 2.14), all of which are predators or competitors of fish larvae. Larval fish concentration was higher at low concentrations of trachymedusae, chaetognath, ephyrae, calanoid copepods and siphonophores. Most other groups explained very little variance (Figure 2.14).

During the day, five taxa explained over 80% of the 60.4% explained variance: siphonophores (Calycophorae) 20.8%, trachymedusae 18.5%, ephyrae 17.4%, appendicularians (Oikopleuridae) 15.9% and chaetognaths 11.2% (Figure 2.14). Again, all are predators or competitors, except for appendicularians (Oikopleuridae) that are potential prey. Larval fish concentration was higher at low concentrations of siphonophore (Calycophorae), trachymedusae, ephyrae, appendicularians (Oikopleuridae) and chaetognaths; and higher at high concentrations of calanoid copepods. Relationships with other taxa were weak (<5%; Figure 2.14).

2.4 DISCUSSION

2.4.1 *Remarks on the sampling design*

The high variability of the hydrological structure of the front showed the importance sampling hydrology and biology simultaneously. Indeed, trying to relate the distribution of fish larvae to the front structure explored just a few days earlier, which was ~10 km more coastal, would have led to major misunderstandings. For example, many coastal fish larvae would have been thought to be distributed in the central zone, where few to no larvae occurred.

Both sampling methods (ISIIS and plankton nets) provided a similar picture of the horizontal distribution of fish larvae along the transect (Figure 2.7) but nets provided fine taxonomic resolution while ISIIS provided detailed spatial (in particular vertical) resolution. Combining these two methods allowed to take advantages of the strengths of both techniques (as already suggested [141]). Here, using only ISIIS data with no taxonomical resolution, would have resulted in missing the delimitation of coastal fish larvae distribution. Conversely, plankton nets, even depth-stratified ones, would not have uncovered the fine scale patterns of vertical distribution and relationships with other taxa that ISIIS allowed.

In terms of cost-benefit, identifying both fish larvae and zooplankton groups from the 19 plankton net samples required approximately one man-month, while manually processing the twenty casts sampled with ISIIS demanded six man-months. Given the higher effort required to process high-frequency imaging data, this method

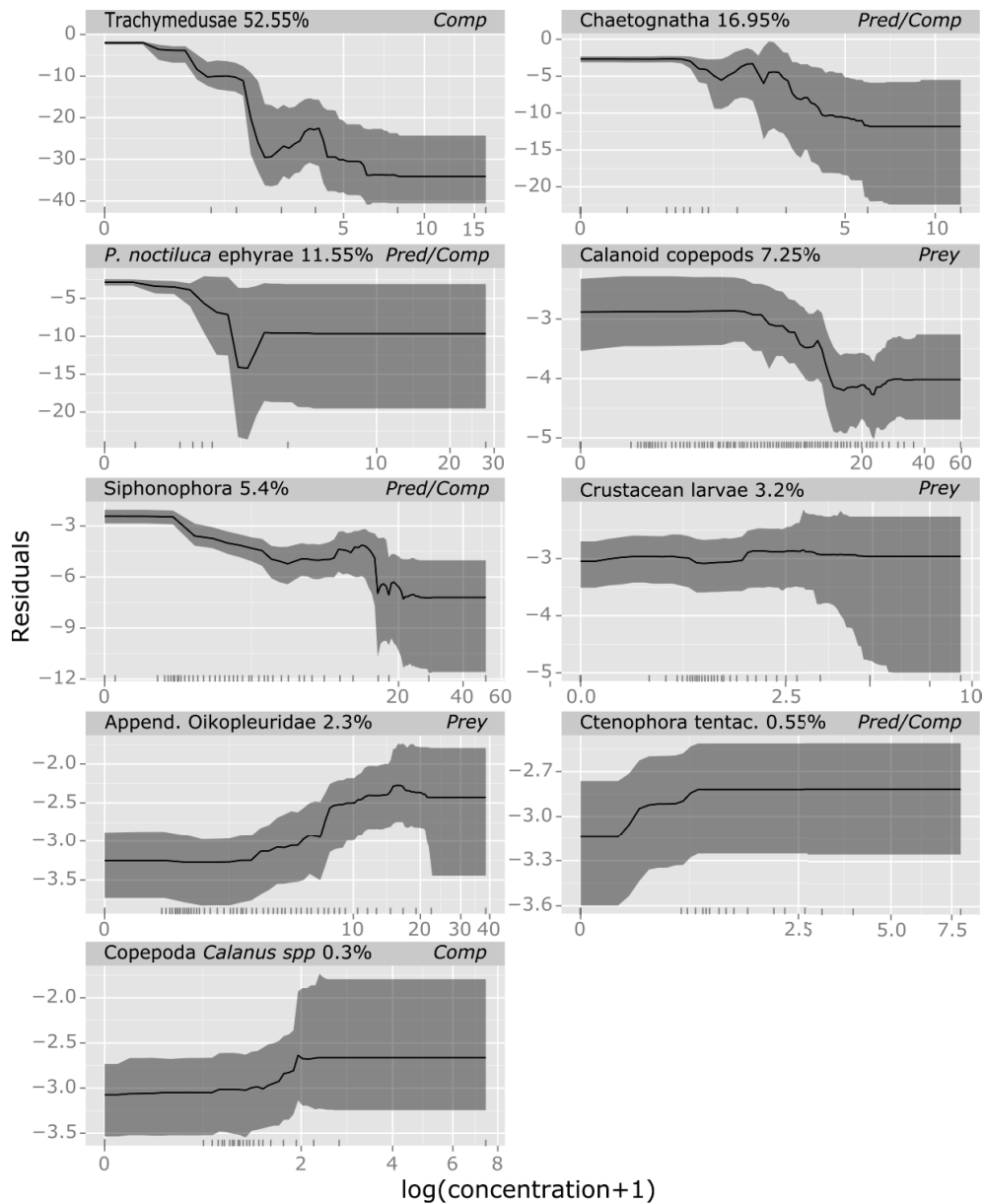


Figure 2.14: Effect of zooplankton concentrations on larval fish concentrations during the night transect (*biological BRT*). Zooplankton concentrations are $\log(n+1)$ transformed for the plot, to better spread the data. Taxa are ordered in decreasing order of influence (decreasing proportion of explained variance). Labels indicate their role relative to fish larvae (*Prey*, *Comp*: competitors and *Pred*: predators).

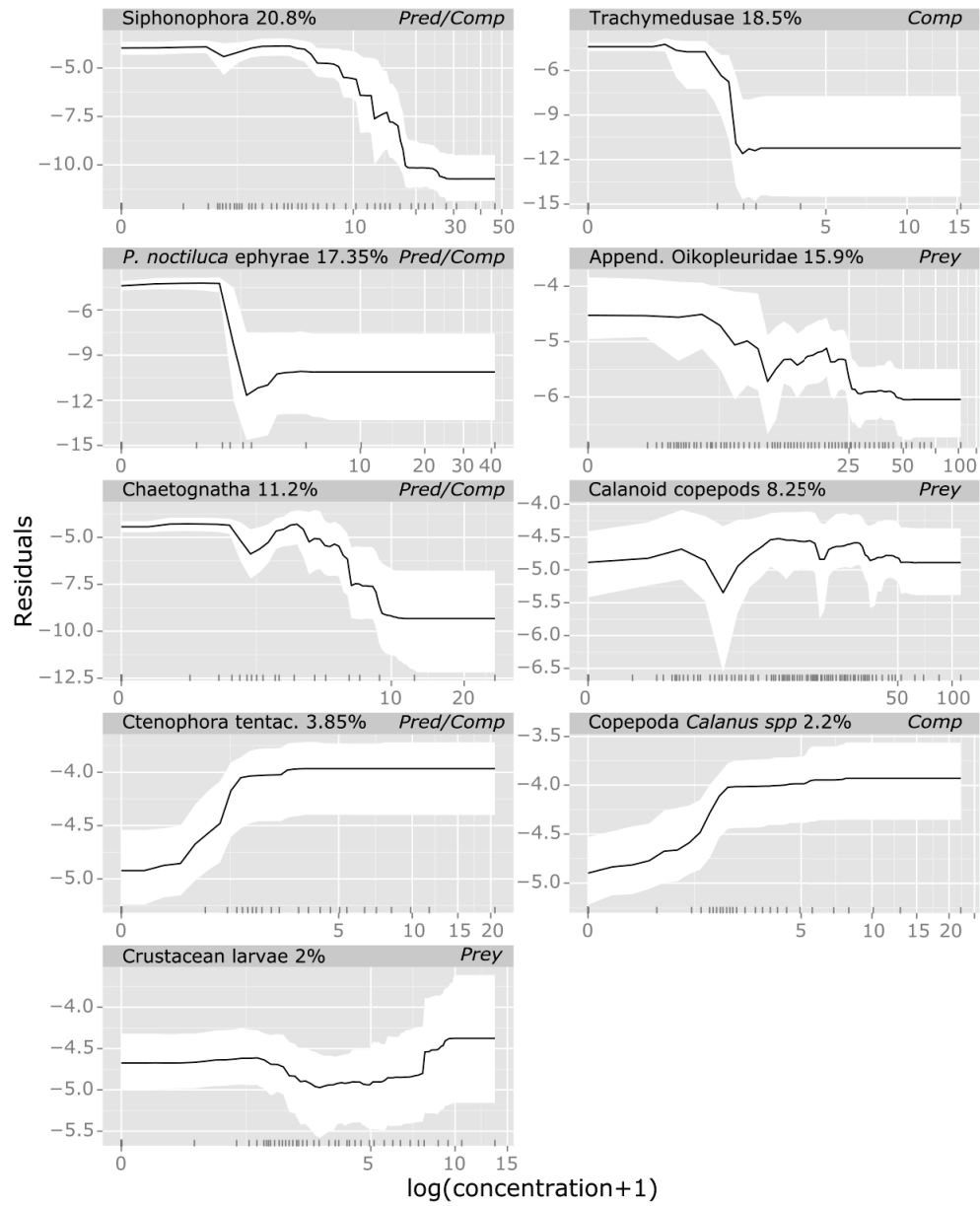


Figure 2.15: Effect of zooplankton concentrations on larval fish concentrations during the day (*biological BRT*). Same conventions as Figure 2.14.

should be focused on questions unresolvable by plankton nets, such as microscale distribution of fish larvae and their relationships with other taxa, but should not aim at replacing plankton nets.

Only few plankton nets samples were collected, as their original purpose was to inform on the taxa present to then find them again in ISIS images. Fish larvae collected were particularly small (mostly preflexion or flexion stages, total length of 3.6 mm on average) for a mid-summer period in the North-Western Mediterranean and their shadows seen by ISIS not detailed enough for identification, which defeated this purpose. Nevertheless, this study confirmed the usefulness –if not the necessity– of combining the two sampling methods.

2.4.2 *Description of the frontal structure*

During this study, the cross-front sections showcased the characteristic structure described by Prieur *et al.* [143, 145, 172]. The three main zones (coastal, frontal and central) were well differentiated by sharp and oblique isohalines that spread through the thermocline. Oblique convection cells were identified by three downwelling zones of high fluorescence, temperature and oxygen concentration, as schematised on Figure 16. In addition, the offshore side of the current expanded horizontally and moved offshore by ~10 km in just five days (Figures 2.4 and 2.5), denoting intense mesoscale activity in the Ligurian current. The westward component of the core of the jet current reached 48 cm s^{-1} , which is higher than the speed usually observed in summer (30 cm s^{-1} [173]). Added to the marked haloclinic signature of the front and the large variability in the location of the limits between hydrological zones, it confirmed that the current was highly energetic for this time of the year. These observations suggested the presence of large meanders, with wavelength of at least 10 km (i.e. the variability range of the location of the separation between the frontal and central zones), moving at a speed of $\sim 2 \text{ km day}^{-1}$, which concurred with previous descriptions of the propagation of mesoscale meanders in the region (10-100 km wavelengths and up to 10 km day^{-1} propagation [45, 174]).

2.4.3 *Ichthyoplankton distribution explored at multiple scales*

The snapshot sampled across the Liguro-Provençal current showed that, at this time of the year, ichthyoplankton was mostly distributed in the upper 50 m of the water column during both day and night, which is compatible with the observations on the Catalan coast [105]. Fish larvae were concentrated in shallow waters at night and spread

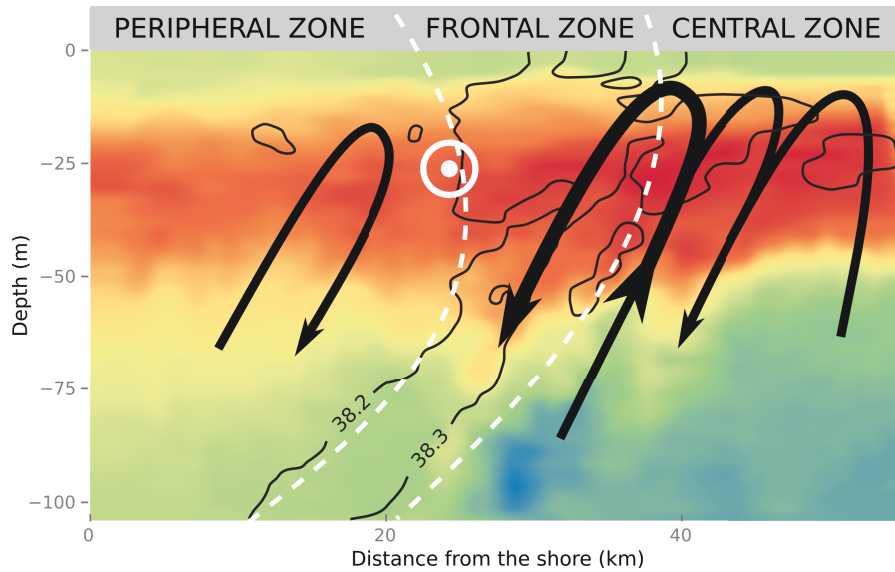


Figure 2.16: **Schematic representation of the structure of the frontal system, overlaid on top of oxygen concentration.** Dashed white lines separate the three main zones. The white circle-dot indicates the location and direction of the core of the Liguro-Provençal current. Black arrows denote the four convection cells, sized to their observed vertical range of influence. Solid grey lines are the 38.2 and 38.3 isohalines.

vertically during the day (downward shift of 22 m; Figure 2.11). This shows a diel vertical “migration” or at least a change in behaviour between day and night. Again, studies conducted off the Catalan coast also showed that Mediterranean larval fish species undertake diel vertical migrations, although over a limited depth range [105, 106, 175].

Very strong patchiness was observed, with often >10 fish larvae per m^3 . These concentrations were five to nine times higher than the maximum values reported in the NW Mediterranean Sea (<2.1 individuals per m^3 [106]). However, this result probably does not indicate that larval fish concentrations are that much higher in the Ligurian Sea than in the Catalan region, but rather that nets, by averaging over larger volumes than ISIIS, underestimate the local concentrations and patchiness of fish larvae. Indeed, the concentrations measured in the Catalan region were diluted over 10 m vertical depth bins [106], while ISIIS data was aggregated on 1 m depth bins here. The most abundant species collected in plankton net hauls was *Engraulis encrasicolus*. This species may account for the dense patches that were observed around 5 m in the night transect, since this species is known to accumulate below the surface at night [176].

Our results also demonstrated the foremost influence of hydrological and hydrographical structures on the horizontal and vertical distribution of fish larvae across the Ligurian front during the sampling period. The vast majority of fish larvae were observed on the coastal side of the current, in waters fresher than 38.25 (Figure 2.11 and 2.13). These sharp thresholds suggested that fish larvae were physically constrained to the coastal side of the front or that they actively controlled their position to remain within a very precise range of preferred salinity levels. Hydrographically, the 38.25 isohaline corresponded to the coastal side of the first major divergent circulation cell, located within the frontal zone (Figure 2.16). It leads to favour the hypothesis that, like echinoderm larvae [148] or other zooplankton taxa in the Ligurian Sea [145, 177] and like fish larvae in the Catalan front [152, 178], most fish larvae observed here were physically retained on the coastal side of the Liguro-Provençal current, even if some were present on both sides of the front and close to or inside the core of the Ligurian current (Figure 2.11).

Conversely to the Catalan region [53, 178], no major accumulation of organisms were observed inside the front, although some patterns point towards a small accumulation where the front met the surface. Indeed, one station located between the frontal and central zones displayed concentrations of *Auxis rochei rochei* larvae and fish eggs higher than neighbouring stations (Figures 2.8 and 2.9). This station matched spatially with the most offshore convergent cell, suggesting that hydrographical conditions may accumulate passive propagules from the frontal and central zones. We cannot draw conclusions regarding the origin of the specimen collected, but in the Mediterranean Sea, *Auxis rochei rochei* favours spawning close to the shore [179] and these larvae were thus unlikely to be spawned in the central zone.

Further comparisons with the Catalan shelf-slope front highlighted other similarities, even if they should be taken with caution due to the limited sampling period of the present study. Pelagic and mesopelagic species were present over the entire cross-front section in both regions [53], although much less abundant in the central zone in this study. Larvae of coastal fish species were constrained to the coastal side of the front in both regions, but were split into markedly different assemblages defined by adults habitat in the Catalan [151, 152, 180] and Balearic fronts [181] while it was not the case here. An assemblage of coastal species could be distinguished from shelf or shelf-slope dwelling species in the Catalan region, here, at this time of the year, the vast majority of species were mixed in a single assemblage, containing coastal, pelagic, mesopelagic and benthopelagic species (Figure 2.10). The continental shelf is very narrow in the Ligurian Sea and may not lead to such different communities of adults. The larval

fish community may thus be mostly influenced by the structure of the front rather than by the location of spawning by the adults (i.e. the adults habitats).

This study provides a first snapshot of the ichthyoplankton distribution across the Liguro-Provençal current, in the Ligurian Sea. Even if most points seem consistent with studies on the Catalan front in summer, the limited sampling period of this study prevents drawing conclusions over larger temporal scales (e.g. month- or year-scale). More extensive studies should therefore be conducted to explore the persistence of the distribution patterns described here over time and under contrasting hydrodynamic conditions.

2.4.4 Larval fish and zooplankton relationships

Like fish larvae, many zooplankton taxa were present in higher concentrations in the coastal side of the front and in the upper 50 m on the water column (e.g. copepods, chaetognaths, siphonophores, *Pelagia noctiluca* ephyrae, trachymedusae). As explained above, most coastal NW Mediterranean fish larvae display limited diel vertical migrations [105, 176, 178, 180] that were shown to match, at least for one species, with the highest concentrations of their potential food (copepodites stages of copepods and nauplii [106]). Here, relationships between fish larvae and two groups of potential prey (crustacean larvae, calanoid copepods) were weak. While fish larvae should be able to feed on crustacean larvae and calanoid copepods in general, the fish larvae here were small (3.6 mm total length on average, mostly preflexion and flexion stages) and the crustaceans seen by ISIIS were only the large ones (2.9 mm and 2.2 mm in length for crustacean larvae and calanoid copepods respectively). These fish larvae could therefore not feed on such large crustaceans. Nauplii and copepodites stages of copepods were too small to be observed with this imaging system. A higher-resolution, smaller-volume camera should be used in order to resolve the distributions of these potential larval fish prey (and the new version of ISIIS is now equipped with one). The third potential prey of fish larvae were Oikopleuridae appendicularians, that, even if less documented, possess the same caloric density as copepods [165]. High concentrations of fish larvae coincided with high concentrations of appendicularians at night (Figure 2.14), but with low concentrations during the day (Figure 2.14). These observations are compatible with a positive selection of appendicularian-rich zones at night, possibly for feeding. This group of appendicularians showed no diel vertical migration and was most concentrated near the surface (*pers. data*), while fish larvae move to shallow depths

at night only (Figure 2.11), which this may explain the low relationships with this group during the day.

Positive or negative, but never neutral, relationships were observed between fish larvae and their predators/competitors (Figures 2.14 and 2.15). The positive relationship with the concentration of tentaculated ctenophores could be the result of the exploitation of similar food sources, as these carnivorous gelatinous zooplankton are huge consumers of nauplii, copepodite stages of copepods and copepods (up to $>90 \text{ ind d}^{-1}$ [169]). All other predators had the expected effect: concentrations of fish larvae decreased when the concentrations of predators increased. These relationships suggest the presence of interactions between fish larvae and zooplankton taxa, which could indicate a top-down control by predators which deplete fish larvae populations; at least ephyrae [62], siphonophores [169], chaetognaths [166] and possibly other medusae predate heavily on fish larvae and were all observed in high concentrations. However, such relationships could also be the outcome of predators avoidance by fish larvae, at microscale, as it was already observed in the shallow waters of the Gulf of Mexico [134]; fish larvae favoured zones with low concentrations of predators, rather than zones with high concentrations of prey but also of predators/competitors.

If fish larvae did not avoid predators or could not detect them, predators would deplete the stock of fish larvae and the relationships between the concentration of fish larvae and their predators would be monotonously decreasing. If larvae actively avoided predators, this behaviour would only occur when predators are numerous, above a threshold concentration. The relationship between fish larvae and predators concentrations should then show this threshold.

Most predators and competitors considered in this study generally feed at night [62, 168–170]. Vision is the most important cue for feeding [163] and for predator avoidance by fish larvae [182]. Fish larvae should therefore avoid predators during the day more than at night. Figures 2.15 and 2.14 suggest a threshold effect for Calyphorae siphonophores ($>10 \text{ individuals.m}^{-3}$), *P. noctiluca* ephyrae ($>5 \text{ individuals m}^{-3}$), chaetognaths ($>7 \text{ individuals m}^{-3}$) and Trachymedusae ($>2 \text{ individuals m}^{-3}$) more marked during the day than at night, leading to favour the hypothesis that fish larvae may avoid zones of high concentrations of predators and competitors when they are able to detect them.

2.5 CONCLUSIONS

By combining two complementary sampling methods, this study provided an initial description of the distribution of fish larvae across

a section of the Ligurian current. High concentrations of the young fish larvae observed here were limited to the coastal side of the Ligurian front, likely by physical constraints. The high-frequency imaging method enabled to highlight that patches of fish larvae were likely to be denser than previously described in the NW Mediterranean Sea using plankton nets.

Theoretical studies suggest that feeding success of fish larvae may be higher than previously thought, even at low prey concentrations [61], while predation may probably the most important cause of mortality in young larval fishes [41, 61]. Here, the concentration of small predators indeed seemed to influence the distribution of fish larvae more than the concentration of prey. However, empirical studies in the natural environments of fish larvae are still lacking [15], partly because *in situ*, high-frequency and high-resolution instruments are required to detect such interactions. In the present study, not all potential prey of fish larvae could be captured, nor could large predators such as adults of *Pelagia noctiluca*. Nonetheless, it revealed relationships that suggest interactions between fish larvae and their potential prey/predators/competitors at microscale (<1 m), indicating that even preflexion and flexion fish larvae may be able to control their vertical position to optimise their microscale environment. The limited frontal accumulation, the presence of diel vertical migrations and the predators avoidance behaviour all hint that behaviour of fish larvae may be an important factor shaping their distributions and overall survival.

IMPERFECT AUTOMATIC IMAGE CLASSIFICATION SUCCESSFULLY DESCRIBES PLANKTON DISTRIBUTION PATTERNS

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3.1 INTRODUCTION

As explained in Chapter 2, hydrodynamics and hydrological structures drive the mesoscale distribution of organisms in the oceans, submesoscale processes are determined by the interaction between biological and physical processes, while most biological interactions (predation, competition, etc.) occur at microscale.

Imaging techniques can provide valuable information about the *in situ* microscale distributions of organisms [e.g. Chapter 2; 109, 128] but they quickly generate very large datasets of images. The *In Situ* Ichthyoplankton Imaging System (ISIIS), the instrument used in Chapter 2, generates about 52,000 four megapixel (2048 x 2048 pixels) frames per hour. Over a 10-day cruise, part of which is presented in Chapter 2, 96 hours of ISIIS amounted to about five million frames (21 TB of data) containing an estimate of at least 25 million objects of interest, large enough to be identified. Manually processing such big datasets has to be limited to few groups of interest [e.g. 128, 134, 142, 183] and still remains time prohibitive. Developing accurate automatic identification processes for such big datasets is still a challenge [141, 184, 185] that needs to be solved in order to fully resolve microscale processes.

Imaging data are typically handled in a three-step process: first, detecting and segmenting relevant objects (or regions of interest) from raw images; then measuring features of each object (such as size, aspect ratio, etc.); and finally using these features to classify the objects into biologically/ecologically relevant groups through machine learning algorithms. Several automatic identification procedures have already been applied to small plankton (up to a few thousand images)

using various classifiers: Random Forest [e.g. 186], Support Vector Machines [e.g. 187], Bayesian models [188] or neural networks [e.g. 189]. Some also combined several classifiers to improve prediction accuracy [187, 190, 191]. While the algorithms differ, all these classifiers have in common the fact that they can compute a score (often a probability) for a particle to be in *each* class. The class with the highest score is then chosen as the predicted class and that is often the only information that is retained from the classifier. So, while classification is typically viewed as a yes-or-no problem, the real outputs from the classifiers are actually more continuous.

Here, we focused on *Zooprocess* and *Plankton Identifier (PkId)* [158]: an image processing and identification toolchain that was first developed for the *Zooscan* (a laboratory plankton scanner) and then extended to the UVP [137] and other imaging systems as described in the Chapter 2. From the full image, *Zooprocess* segments objects and computes a set of descriptive features (grey levels, length, width, area, shape, etc.) that are then used by *PkId* through various classification algorithms (Support Vector Machine, Neural network, Random Forest, etc.), although Random Forest has proven to be the most accurate and is now used routinely [158]. This software suite is widely distributed worldwide and used in 60 research teams over five continents (e.g. France [192]; China [193]; Brazil [194]; USA [195]; Mozambique [196]; New-Caledonia [197]; Antarctica [198]). It is most commonly used as a *computer-assisted* identification system, whereby the classifier proposes identifications that are then all validated by human operators.

Zooprocess and *PkId* offer appropriate tools to handle ISIIS data but the number of images generated by ISIIS (typically several million millimetre-scale objects in a few hours of sampling) makes human validation time-consuming. For example, the full validation of 1.5 million objects to create a reference, true dataset that was used in Chapter 2, took seven man-months. However, given the size of that data, even a subset is likely to contain relevant ecological information. Here, we propose to filter out objects with a low classification score (i.e. the most likely wrong identifications) and assume that all remaining objects are correctly classified, hence removing the validation step. While other studies have compared automatic classification efficiency between methods using only classification metrics (e.g. precision, recall, etc.; [187, 199, 200]), we suggest that it is more biologically relevant to examine whether the same ecological patterns can be detected in the reference dataset and in the predicted, filtered but not validated dataset (hereafter *predicted dataset*). In this study, we specifically explore the fine scale spatial distribution of zooplankton

and ichthyoplankton across a frontal structure, as well as their diel vertical migration patterns in those two datasets.

3.2 MATERIALS AND METHODS

3.2.1 *Test samples*

The test samples are the data presented in Chapter 2, in which the imaging instrument, ISIIS, and the sampling design have been thoroughly described. In short, ISIIS was deployed for two transects across the Liguro-Proçençal current, a coastal jet that creates a permanent, mesoscale front and delimitates a coastal, a frontal and an offshore zone, identifiable in both hydrological variables [174] and biological communities [147]. One transect was conducted at night, the other during the following day, in July 2013. ISIIS sampled the water column in a tow-yo fashion, between the surface and 100 m depth.

3.2.2 *Learning set and classification*

The image pre-processing and segmentation have been described in Chapter 2 (Section 2.2.2, p. 49). In short, the segmentation process extracted the so-called Regions Of Interest (ROI), that is to say the abiotic particles and the organisms that were seen by ISIIS. Forty-six features were measured on these ROI, including their transparency (five measures of grey levels: mean, mode, standard deviation, minimum, maximum, etc.), their size and shape (length of the minor and major axes of the best fitting ellipse, Feret diameter, circularity, symmetry) and aspect (grey level histogram descriptors such as skewness, cumulative histograms, etc.). However, the classification method, which is at the centre scope of this chapter, is detailed.

Supervised classification techniques require a set of classified and measured objects to learn the differences between the classes based on their features. The learning set comprised 14 classes (Figure 3.1) with a target size of 200 objects per class, a number which proved to be appropriate for previous *Zooprocess/PkId* projects [158]. In total, the learning set contained 5979 objects. They were chosen to be representative of the diversity of each class but with a bias towards the start of the first (night) transect, because images were processed in order of collection and the learning set was started as soon as the first images became available.

All 1.5 million objects were classified into these 14 biotic and abiotic classes using a Random Forest classifier working on the 37 features measured by *Zooprocess* complemented by 9 new variables, computed

from the original features by *PkId* (aspect ratio, elongation, etc.). The parameters of the classifier were left at their appropriate defaults in *PkId*: 100 trees, bagging of 1, 6 features randomly selected per tree, leaf size of 2 objects.

Finally, three trained experts validated the classification of each object, yielding a completely identified dataset of 1.5 million objects (reference dataset).

3.2.3 Data filtering and optimisation of the classifier precision

To detect true ecological patterns from a predicted class, one needs to be confident that this class is composed of objects of the correct ecological group. In terms of classifier performance, we want high precision (precision = proportion of correctly classified objects in a predicted class). With low precision, a predicted class would actually be a mix of various organisms, from which no meaningful conclusion can be drawn. In addition, with large datasets, not *all* objects of a class need to be collected to detect patterns; a *subset* of the total may be enough. In terms of classification, it means that we may be able to afford a low *recall* (i.e. proportion of the total number of objects of a class that are predicted in that class). To test this hypothesis, we filtered out the most likely mistakes to increase precision, at the cost of potentially also removing some correctly classified objects (hence decreasing recall) and then inspected the resulting dataset.

The probabilities for each object to be in each class were used as the filtering criterion. In each class, a threshold probability was set. All objects with probability above the threshold were kept and assumed to be correctly identified; other objects, with probability equal to or lower than the threshold, were considered to be potentially wrong and were discarded. Since precision needed to be controlled (and high), thresholds were set to target a given precision. For example, picking as threshold the probability of the first wrongly identified object results in 100% precision (all objects ranked above the first false positive are correctly classified). Here, an error rate of 1% was deemed acceptable. In each class, objects were manually screened in decreasing order of probability; the screening stopped and the threshold was set when 1% of the objects screened so far were wrongly identified ones.

The computation of thresholds was done with the training set only, because in operational conditions, only the identifications of the objects in the training set are known. The class probabilities of each object in the training set were predicted using 2-fold cross-validation repeated 50 times, using the Random Forest procedure described above. The probabilities were averaged over the 50 repetitions and

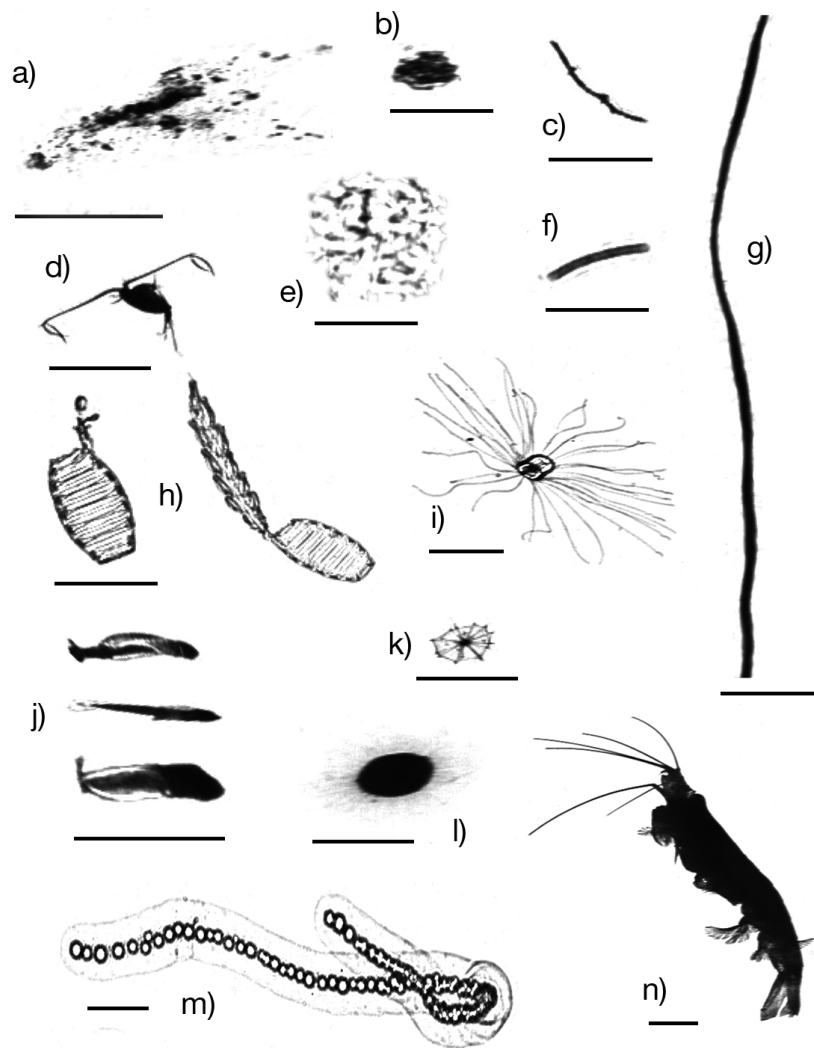


Figure 3.1: Example of organisms taken from the classes of the learning set; each image has a scale bar of 5 mm. a) *Light aggregates*: marine snow composed of larvacean houses, mucus, etc.; b) *Dark aggregates*: solid, opaque marine snow; c) *Fibres*: thin fibres and faecal pellets; d) *Copepods*: mainly calanoid copepods; e) *Noise*: noise generated by water density changes; f) *Diatom chains*: phytoplankton, diatom chains; g) *Tentacles*: *Pelagia noctiluca* tentacles; h) *Doliolids*: thaliaceans of the family Doliolidae with and without tail; i) *Trachymedusae*; j) *Fish larvae*, from top to bottom: Engraulidae, Myctophidae, Carangidae; k) *Acantharians*: solitary radiolarians of the family Acantharia; l) *Radiolarians solitary*: solitary radiolarians of the family Colodaria; m) *Radiolarians colonies*: colonies of radiolarians of the family Colodaria; n) *Shrimps*: Mysidaceae or Euphausiacea.

objects were assigned to the class of highest probability. In each predicted class, thresholds were computed as explained above: objects were screened in decreasing order of probability and the threshold was set when 1% of mistakes was reached.

The probability thresholds computed on the learning set were applied to the predictions of the 1.5 million objects and the subset that was kept constituted the “predicted dataset”. Thus, once the identification of objects in the training set are known (which is required for prediction anyway), the rest required only computation, no further human validation effort.

3.2.4 *Consequence of data filtering on classification metrics*

By construction, the chosen thresholds resulted in exactly 99% precision on the training set. Because the identification of all 1.5 million objects in the reference set was known, the precision, recall and F1 score ($2 \times \textit{precision} \times \textit{recall} / (\textit{precision} + \textit{recall})$) could be computed for each class over the whole dataset, before and after the filtering process. This allowed us to check whether the precision after filtering approached 99% on the whole dataset as well and how much this improvement in precision cost in terms of decrease in recall.

3.2.5 *Statistical comparisons between the reference and predicted datasets*

Individual objects were counted over 1 m depth bins along the undulating trajectory of ISIIS and counts were transformed into concentrations by dividing by the volume sampled in each bin. This resulted in maps of the concentration of each class of organism across depth (0-100 m) and distance from the coast (0-60 km) for each transect (e.g. Figures 3.2 and 3.3).

The similarity between the maps for the reference and predicted datasets was assessed using the *t*-test modified by Dutilleul [201] (H₀: no correlation between the maps) as well as the Pearson and Spearman correlation coefficients. The Dutilleul *t*-test takes into account the spatial autocorrelation of the data, based on Moran’s *I*, and is therefore more appropriate to avoid over-estimating the similarity of spatial patterns.

The average vertical distribution was computed for each group and each transect (separating day and night). Reference and predicted vertical distributions were compared with the version of Kolmogorov-Smirnoff test modified by Solow *et al.* [160], which specifically takes into account autocorrelation along depth caused by the patchiness of plankton.

Concentrations were necessarily lower in the predicted dataset because some objects were discarded. Before the comparisons described above, concentrations were normalised to a maximum value of 1 for each of the 14 classes and each transect, by dividing by the maximum concentration recorded. This puts the focus on distribution patterns, rather than actual concentration values, which may be badly estimated if the recall is low.

3.2.6 Comparison of ecological patterns

The front across which the transects have been conducted can be delineated by the 38.2 and 38.3 isohalines [174] and is expected to strongly structure zooplankton communities [e.g. Chapter 2; 145, 148]). Beyond comparing distribution maps numerically, the maps were inspected visually to check whether the ecological interpretation of the patterns relative to the frontal structure would be the same in the predicted data compared to the reference data.

Similarly, beyond just comparing reference and automatically predicted vertical distributions, we assessed whether the range and strength of diel vertical migrations could be as readily detected in the predicted dataset as in the reference dataset. Within each class, day and night distributions were compared with the Solow-Kolmogorov-Smirnov test and the value of its statistic was compared between reference and predicted data. The day-night shift in the barycentre of the distribution was computed with reference and predicted data and also compared.

3.2.7 Data selection

Abrupt changes in water temperature around the thermocline generated large density differences, which are unfortunately well captured on shadowgraphs as those taken by ISIIS. These numerous objects were classified as “Noise”. Another abundant class of objects were tentacles of the medusa *Pelagia noctiluca* that got stuck on ISIIS and were imaged constantly. These two classes of objects are ecologically irrelevant but were abundant and predicted with high precision (>95%). They are both omitted from the subsequent analyses.

3.2.8 Data analysis tools

All data were processed with R (3.1.2) [171] with packages *plyr* (1.8.1) and *dplyr* (0.4.1) for data manipulation, *ggplot2* (1.0.1) for plotting, *randomForest* (4.6.10) for image classification, *SpatialPack* (0.2.3) for com-

paring spatial distributions, as well as custom code for the modified Kolmogorov-Smirnov test, the Z_{cm} and S_{cm} computation.

3.3 RESULTS

3.3.1 Consequences of data filtering on classification metrics

The process of filtering out low probability objects considerably increased the precision (by 37% on average; Table 3.1). While probability thresholds were set to yield 99% precision on the cross-validated learning set, precision was lower on the reference dataset. This is to be expected because the 6000 images in the learning set cannot fully represent the variability in the whole dataset (1.5 million images). Still, the average precision of biological categories was 84%. The Trachymedusae and Acantharia radiolarians displayed the lowest precision (61.9% and 65.4% respectively), but it was still vastly improved over the 9% and 7% (respectively) in the raw prediction.

Table 3.1: **Classification metrics before and after filtering out objects with low prediction confidence:** percentage of data kept after filtering; precision, recall and F1 score before and after filtering and difference (after - before). Improvements (positive differences) are in bold. Non-living groups are presented first, groups of biological interest second.

Class	Precision			Recall			F1		
	% kept	before	after diff	before	after	diff	before	after	diff
Dark aggregates	9.9	77	95 19	50	7	-43	60	7	-54
Light aggregates	24.1	8	17 9	53	4	-49	14	4	-10
Fibers	8.5	46	85 38	56	7	-49	51	7	-44
Copepods	16.6	54	88 34	72	22	-49	62	22	-39
Doliolids	35.9	80	95 16	64	40	-24	71	40	-31
Fish larvae	14.9	12	80 67	62	23	-39	21	23	3
Trachymedusae	32.0	9	62 53	79	51	-29	16	51	35
Diatom chains	34.2	75	97 22	72	29	-43	73	29	-45
Radiolarians Acantharia	13.6	7	65 58	74	19	-55	14	19	5
Radiolarians colonies	21.6	24	94 70	62	17	-45	35	17	-18
Radiolarians solitary	63.7	68	88 19	89	66	-23	77	66	-12
Shrimps	55.6	51	89 38	74	53	-21	60	53	-7

To get to these precision levels, over 70% of the objects need to be filtered. The percentage of objects retained ranged from 8.5% for fibres to a maximum of 63.7% for solitary radiolarians. As a consequence, on average, filtering decreased the recall by 39% and the

F1 score by 7.8%. However, the improvement in precision dominated the effect of the decrease in recall, because the classification accuracy of the whole dataset improved from 40.2% to 56.3% after filtering.

3.3.2 *Description of the spatial distribution of plankton with respect to the front*

The automatically predicted and filtered spatial distributions of most taxa and particles were significantly correlated with the true, reference distributions in 20 of the 22 groups at the $p < 0.001$ level (Table 3.2; e.g. Figure 3.2). Correlation coefficients were also very high (7 classes with $r > 0.7$ and 8 additional classes with $r > 0.5$). The only two exceptions are fish larvae and shrimps in the day transect, both of which were very rare.

At the 99% precision filtering level, the filtering of fish larvae and fibres on the predicted dataset was so drastic (14.9% and 8.5% of objects left) that the resulting spatial distributions are very sparse and could easily be detected visually (Figure 3.3). Still, even in those cases, the locations of the maximum concentration zones were properly captured in the predicted dataset; there are just too few objects to represent the finer patterns (Figure 3.3).

The reference spatial distributions showed that most taxa were strongly influenced by the frontal zone (Figures 3.2 and 3.3): fish and doliolids were constrained on the coastal side, diatom chains were more abundant in the deep offshore zones and copepods were slightly more concentrated in the upper layers on the coastal side. The high spatial resolution of the data allowed the detection of smaller scale patterns such as a region of slightly lower concentrations of copepods and solitary radiolarians at the front (around 30 m depth for copepods and 50 m depth for radiolarians; Figure 3.2). Solitary radiolarians were also shallower in the central zone compared to the coastal zone and precisely followed the deep chlorophyll maximum (Figure 3.2).

All these patterns, including the contrasts between taxa and the fine-scale low concentration regions at the front, could also be well detected on the predicted data. The conclusions and ecological interpretations on the spatial distribution would be the same. In addition, when the automatic method gave poor results, the sparseness of the resulting data was obvious when visually inspecting the distributions. Coupled with the proportion of discarded images, it enabled to detect poorly predicted taxa even without considering the reference distributions (Figure 3.3).

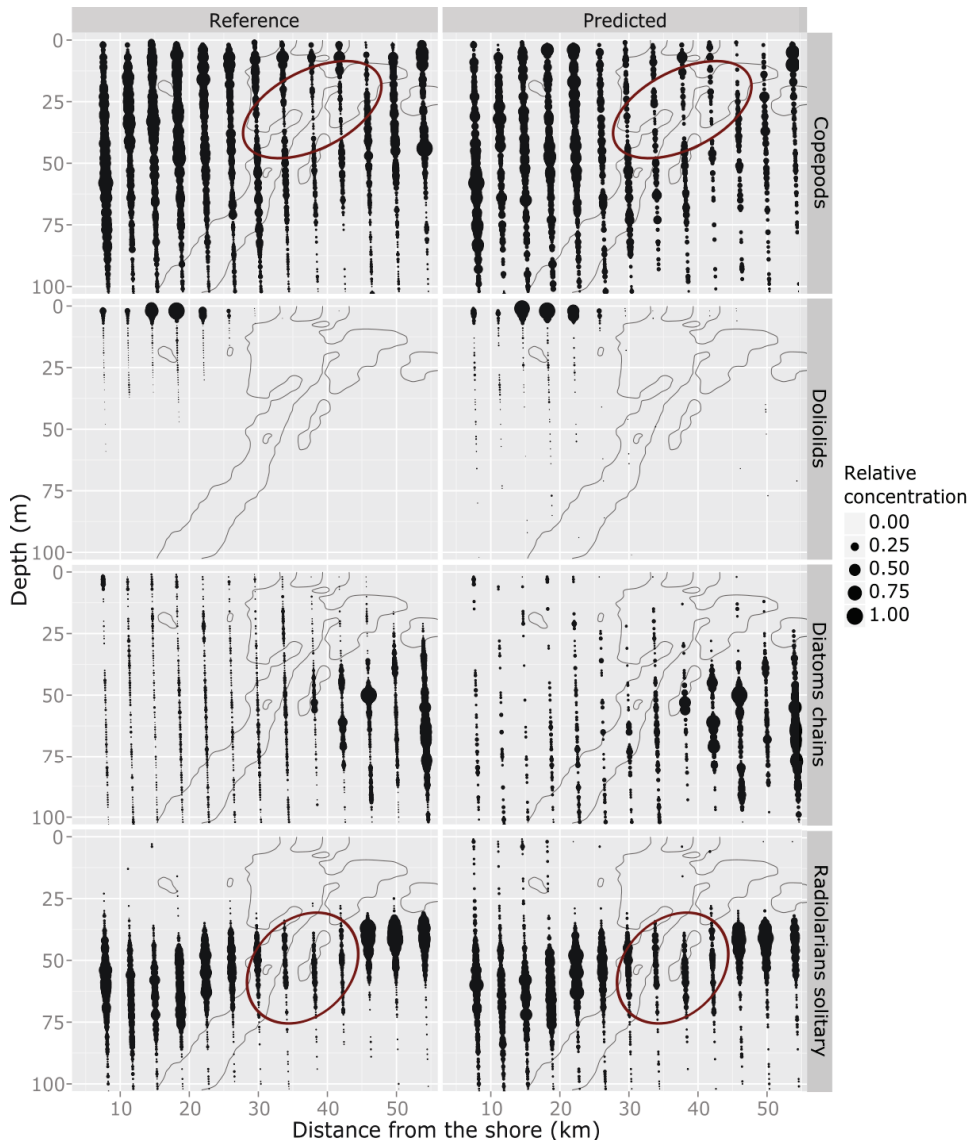


Figure 3.2: Examples of spatial distributions in the predicted dataset (right) that are well correlated with the reference dataset (left). From top to bottom: copepods, doliolids, diatom chains and solitary radiolarians, all during the night transect. The x axis is the distance from the coast (coastal side on the left, offshore side on the right). Grey solid lines are the 38.2 and 38.3 isohalines that delineate the frontal zone. Ellipses represent regions of lower concentration located in the frontal zone. Concentrations were normalised per taxa between 0 and 1 (1 being the highest observed concentration of each taxa).

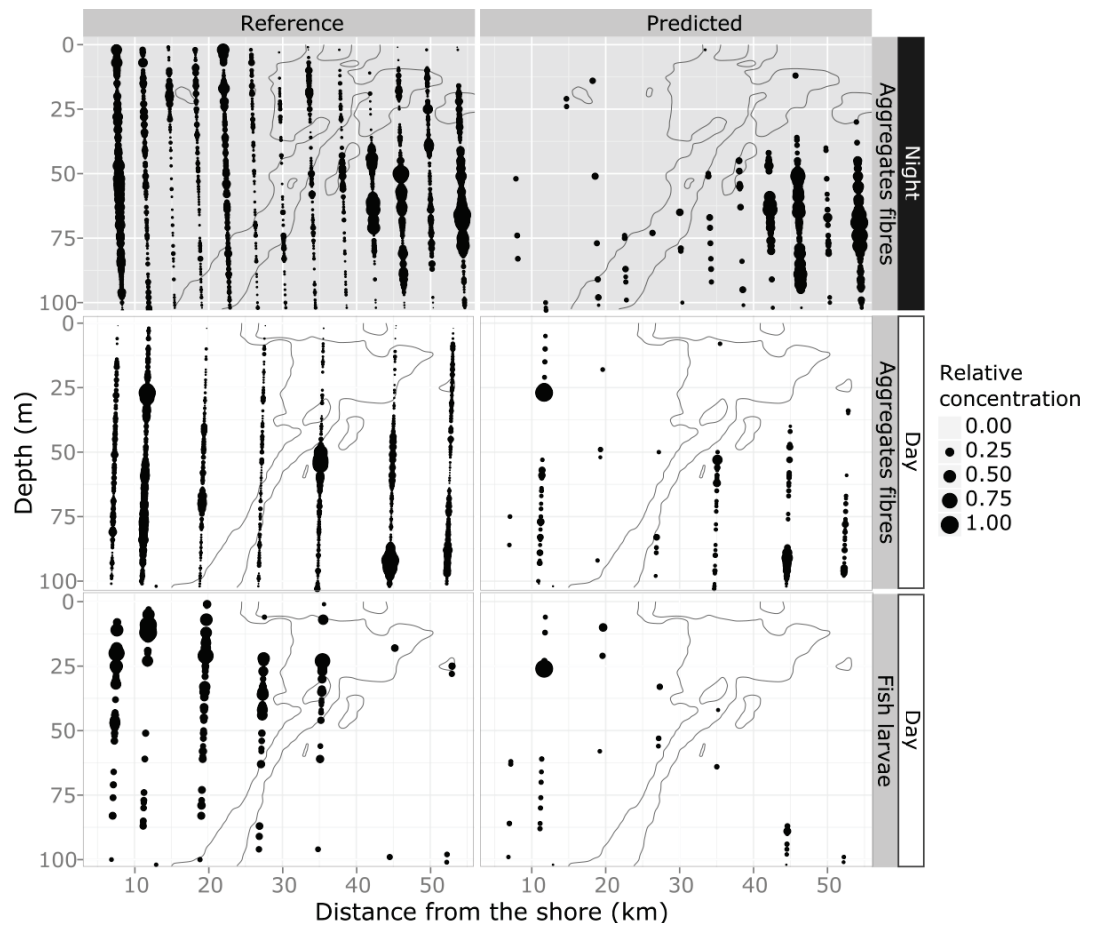


Figure 3.3: Examples of poorly predicted spatial distributions (right) compared to the reference distributions (left). From top to bottom: fibres at night, then during the day and fish larvae during the day. Same conventions as Figure 3.2.

Table 3.2: **Statistical comparisons of spatial distributions between the reference and predicted datasets with three statistics:** Dutilleul modified t -test (statistic, recomputed degrees of freedom and p -value), Pearson's correlation coefficient (r) and Spearman's rank correlation coefficient (ρ). The p -value of dissimilar distributions are in bold.

Class	Transect	Dutilleul t -test				
		F-stat	DoF	p-value	r	ρ
Dark aggregates	Night	29.99	35.28	<0.001	0.66	0.68
	Day	24.11	19.88	<0.001	0.68	0.74
Light aggregates	Day	10.05	75.72	<0.01	0.11	0.34
	Night	103.22	154.59	<0.001	0.38	0.62
Fibers	Day	144.93	190.63	<0.001	0.42	0.62
	Night	54.37	35.89	<0.001	0.74	0.71
Copepods	Day	36.50	28.46	<0.001	0.73	0.71
	Night	12244	274.97	<0.001	0.66	0.94
Doliolids	Day	27064	186.52	<0.001	0.55	0.94
	Night	231.25	161.87	<0.001	0.44	0.77
Fish larvae	Day	1.58	561.37	0.21	0.09	0.05
	Night	286.28	167.98	<0.001	0.61	0.78
Trachymedusae	Day	130.66	286.55	<0.001	0.48	0.55
	Night	431.64	74.13	<0.001	0.72	0.92
Diatom chains	Day	377.12	97.13	<0.001	0.75	0.86
	Night	130.32	176.41	<0.001	0.53	0.64
Radiolarians Acantharia	Day	107.86	166.85	<0.001	0.47	0.65
	Night	220.39	357.97	<0.001	0.61	0.64
Radiolarians colonies	Day	116.20	393.12	<0.001	0.52	0.49
	Night	107.11	22.24	<0.001	0.91	0.89
Radiolarians solitary	Day	101.06	14.33	<0.001	0.92	0.91
	Night	685.26	893.08	<0.001	0.72	0.82
Shrimps	Day	0.01	719.25	0.91	0.00	0.00

NB: No *light aggregates* were identified at night.

3.3.3 Day and night vertical distributions

In 8 of 12 groups, there were slight but significant differences in the predicted vertical distributions versus reference vertical distributions (Solow-Kolmogorov-Smirnov test, $p < 0.05$; Table 3.3). The four groups showing no statistical difference between predicted and reference vertical distributions were doliolids, Acantharia radiolarians, colonial radiolarians and shrimps, although the lack of significant difference in this later case is probably due to a low overall numbers of shrimps.

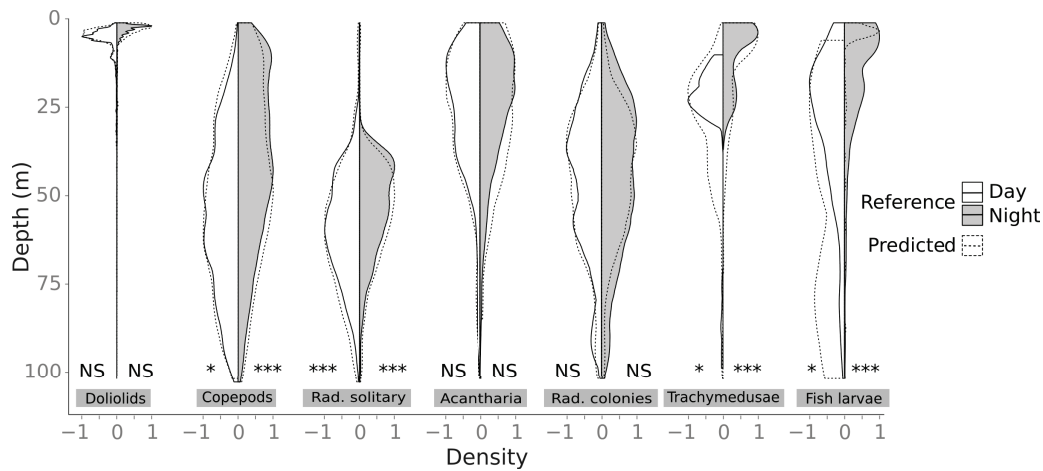


Figure 3.4: **Vertical distribution of various classes during the day (left side) and at night (right side, shaded) as depicted in the reference, validated dataset (solid), and in the predicted dataset (dashed).** The significant levels between reference and predicted distributions are indicated for both day and night (NS: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$). All taxa plotted migrate downward during the day, except for radiolarians colonies and Acantharia that do not migrate.

The shapes of the predicted and reference vertical distributions were often very similar (Figure 3.4: e.g. Radiolarians solitary; but see fish larvae for a counter example). The ecological conclusion regarding depth spread and preferendum would therefore be the same, even when some distributions were considered as statistically different given the high statistical power of the test and large amount of data. In addition, when a significant diel vertical migration could be detected in the reference dataset, it was also significant in the predicted one (Table 3.4). Conversely, colonial and Acantharia radiolarians do not appear to vertically migrate and this conclusion was also reached with the predicted dataset. The ranges of downward migration of Trachymedusae, solitary radiolarians and doliolids were also very comparable between the datasets; the same was true, to a lesser extent, for calanoid copepods (Table 3.4, Figure 3.4). However, the vertical migration of fish larvae was poorly predicted, with a bias towards the surface at night that was much greater than in reality (Figure 3.4).

3.4 DISCUSSION

The method presented here aimed at avoiding the manual validation of predicted identifications by filtering out objects classified with low confidence, hence improving precision (but decreasing recall) and po-

Table 3.3: **Statistical comparisons of vertical distributions between the reference (Ref.) and predicted (Pred.) datasets.** The Solow-Kolmogorov-Smirnov test was used and its statistic and p -value reported. Many predicted vertical distributions were statistically different from the reference distribution. Distribution not significantly different are in bold.

Class	Transect	Solow K-S		Depth	
		Ref.	Pred.	Ref.	Pred.
Dark aggregates	Night	3.91	<0.0001	49.1	55.3
	Day	3.22	<0.0001	41.2	53.1
Light aggregates	Day	2.98	<0.0001	29.0	40.5
Fibres	Night	3.97	<0.0001	61.8	69.7
	Day	1.61	0.005	51.5	69.3
Copepods	Night	2.97	<0.0001	56.1	55.1
	Day	1.44	0.025	40.8	44.9
Doliolids	Night	0.67	0.57	7.1	8.6
	Day	0.82	0.34	5.1	6.9
Fish larvae	Night	1.86	<0.0001	32.6	52.2
	Day	1.25	0.049	16.9	10.9
Trachymedusae	Night	1.44	0.008	25.9	29.5
	Day	1.31	0.020	10.5	12.7
Diatom chains	Night	3.67	<0.0001	64.3	67.8
	Day	1.72	0.001	57.5	63.1
Radiolarians Acantharia	Night	1.13	0.13	28.3	29.9
	Day	0.69	0.61	25.3	27.1
Radiolarians colonies	Night	1.20	0.09	45.8	46.3
	Day	0.51	0.90	45.4	44.4
Radiolarians solitary	Night	2.43	<0.0001	59.3	60.9
	Day	2.23	<0.0001	53.5	55.9
Shrimps	Night	1.00	0.20	49.9	44.1
	Day	0.51	1.00	55.3	53.8

tentially allowing the detection of ecologically meaningful patterns. The precision increase (+37%) was counter-balanced by a recall decrease (-39%), but overall classification accuracy using this method increased by 16%. Studies on laboratory imagery of plankton have usually achieved higher accuracy and could resolve a higher number of groups (e.g. 22 phytoplankton groups [202]; 25 zooplankton groups [200]: 10-20 groups, summarised in [184]) than studies based on images of zooplankton captured *in situ* (e.g. 3 groups with SVM, achieving 80% accuracy [199]; 7 groups with random subspace model

achieving >90% precision but on the trained dataset [191]; 5 and 7 groups with neural networks, reaching 60 to 80% accuracy [187, 189]). The present classifier dealt with 14 groups and reached 56.3% general accuracy as well as 84% precision on biological groups. This falls within the higher range in terms of precision and number of predicted groups compared to previous *in situ* studies on zooplankton. While there is still room for improvement in the final classification rates, the data filtering method presented in this study markedly improved the performance of the standard Random Forest classifier.

Table 3.4: **Comparison of the resolution of diel vertical migration patterns in the reference and predicted datasets.** For each dataset are reported: (i) the statistic (K) of the Solow-Kolmogorov-Smirnov test comparing day and night (bold when the test is significant), which quantifies the overall difference in distribution, and the significance of the diel vertical migration (values in bold) and (ii) the difference between the depth centre of mass at night and during the day, a proxy of the migration range (negative means downward migration during the day).

	Solow-K-S			
	day~night (K)		Migration range (m)	
	Reference	Predicted	Reference	Predicted
Copepods	4.10	2.86	-15.3	-10.3
Doliolids	1.16	1.14	-2.1	-1.7
Fish larvae	1.88	1.72	-15.8	-41.4
Trachymedusae	1.72	2.07	-15.4	-16.8
Diatom chains	2.53	2.25	-6.8	-4.7
Radiolarians Acantharia	0.99	1.15	-3.0	-2.9
Radiolarians colonies	0.50	0.67	-0.4	-1.9
Radiolarians solitary	3.04	2.75	-5.8	-5.0
Shrimps	0.83	0.81	5.4	9.6

Large image datasets are likely to become increasingly common thanks to the development of affordable high-frequency, high-resolution cameras like the one installed on ISIIS. In such big datasets, all the information may not be essential and some may be efficiently omitted [199]. The filtering approach used in this study considerably subsampled the data (72% of objects were discarded) in order to focus only on well-predicted objects. Despite this high subsampling rate, the two dimensional and to a lesser extent vertical, distributions of many classes were not significantly different between the subsampled and the total, reference dataset. In addition, the poorly predicted groups could be easily identified with the sparseness of their predicted distribution and/or to the high proportion of discarded im-

ages (>90%). This provided an additional control for the validation of automatically predicted distributions.

What is more important is that analysing both the reference and predicted datasets for *relevant biological questions* resulted in the same conclusions. They highlighted the foremost influence of the frontal structure, marked by a salinity gradient, on the distributions of organisms across transects. This is consistent with many studies from the literature [145, 146, 148] and was presented in detail in Chapter 2. For example, some taxa like Acantharia radiolarians, Trachymedusae and larval fishes were mostly observed in the coastal or frontal zones and in the upper 50 m of the water column, the only locations where salinity levels drop below 38.2 (Figures 3.2 and 3.3). Diatom chains were most abundant in the deeper layers of the central zone, where copepod concentrations were the lowest, suggesting a possible influence of grazing. These results suggest that species-environment relationships or interspecific interactions can be studied at the very fine scales that imaging techniques provide without requiring labour-intensive validation.

Changes in vertical distributions between day and night, even over less than 10 m, could also be detected in the predicted data for most taxa, with a power and resolution similar to that of the reference dataset (Figure 3.4, Table 3.3). Diel vertical migrations of copepods and medusae are well described in the literature [e.g. 62, 203]. However, the apparent ~5 m vertical movements of Colodaria radiolarians solitary or the 2 m downward displacement of doliolids during the day are not documented in prior studies, possibly because they were missed by other less resolving sampling methods. The ecological significance of these small scale vertical movements was not within the scope of this study but the fact that they could be detected highlights the efficacy of both high frequency imaging system and this automatic classification and filtration method in exploring microscale processes in the plankton.

Some taxa share striking morphological similarities that only a trained expert may be able to differentiate. Such resemblances between disparate taxa usually lead to high error rates in the prediction of these groups [200]. Automatic classification methods may never reach the taxonomical resolution achieved by experts, even if both make mistakes [204]. Combined with data filtering, automatic classification can accurately describe spatial distributions when low taxonomical resolution is acceptable, for example to study broad groups that provide an environmental or biological context for a species of interest. Eventually, manual validation could still be required, but focused on a specific taxonomic group. Here, fish larvae were very diverse and appeared similar to appendicularians and chaetognaths

in terms of body size, shape and opacity. As a result, this group was badly predicted and manual classification would still be necessary to tease apart their distribution.

Using the proposed method, the processing of 1.5 million objects required only the manual sorting of 5979 objects (0.41% of the total), mainly from the first sampling profile. It could properly describe ecological patterns but the drastic filtering process led to underestimating the abundances of all groups. These abundances could be corrected by estimating, in each class, the proportion of objects of this class that were filtered out and/or wrongly classified from a blind prediction using a test-set. In operational conditions, this would require the manual validation of randomly selected images of each category of the predicted dataset, thus increasing the effort beyond the learning set. However, during validation, the throughput of a trained operator was about 10,000 objects per day. So a week or two of validation would probably suffice and it would provide some additional control of error rate in the predicted data.

The present method is based on two characteristics shared by all machine learning methods: the use of a learning set to teach the model how to differentiate between classes and the calculation of a score, or probability, for each object to belong to each class. The probability thresholds for the filtering step are computed by cross-validating the learning set and do not require additional manual sorting. In many cases, Random Forest, working on a few dozen features deterministically measured on the object, came out as the most efficient classifier for plankton data [e.g. 158, 186, 200]. However, deep learning methods such as convolutional neural networks (CNNs) are emerging as promising classifiers for a range of image identification problems and already outperform Random Forest [205, 206]. Applying the method described here to classifiers that already achieve a high accuracy may eventually lead to near-perfect automatic classifications without discarding too much information. Such a combination would allow the handling of large plankton imaging datasets that are still challenging to process rapidly and accurately [184, 185], hence providing appropriate tools to explore the fine- and microscale processes occurring in the oceans.

3.5 ACKNOWLEDGMENTS

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Partie II

LE COMPORTEMENT DES LARVES DE POISSONS EN MER LIGURE LORS DE LA PHASE D'INSTALLATION

"I have already drawn attention to another point which might be considered as possibly exerting some influence upon the mortality of fish in the early stages, viz, the passive movement of the larva with the currents. During the first cruise in the Norwegian Sea, I encountered great numbers of young cod fry drifting in the water above the great main depression in this region. It is possible that many individuals perish during such drifting movements: nothing is, however, definitely known as to this. It would be especially desirable to ascertain the extent of such movement, and how far the young fry are able to return, of their own volition, to such localities as offer favourable condition; for their further growth." **Hjort, 1914**

TEMPORAL PATTERNS OF FISH LARVAE
SETTLEMENT IN THE BAY OF VILLEFRANCHE-
SUR-MER, LIGURIAN SEA (NORTHWESTERN
MEDITERRANEAN SEA)

Robin Faillettaz, Philippe Koubbi, Jean-Olivier Irisson

Article to be submitted to
Marine Ecology Progress Series

4.1 INTRODUCTION

Fish larvae suffer mortality levels estimated to be >70% per day during their pelagic phase [15]. By the end of this pelagic phase, they need to reach a coastal habitat to settle (i.e. change from a pelagic to a demersal lifestyle). While survival rates are still low within the first week after settlement [207, 208], the bulk of the mortality occurs during the larval phase and larval supply to coastal habitats have major effects on recruitment (i.e. settlers that survived and metamorphosed into juveniles) and thus on local population dynamics [209]. Monitoring settlement could therefore provide valuable information for fisheries management and conservation [210, 211]. Settlement-stage fish larvae have strong swimming abilities ([100], to be described in Chapter 6 for Mediterranean species) and may avoid regular plankton nets [212–214]. However, light-traps are efficient as sampling these stages [215] and provide consistent results across various locations (e.g. Florida, USA [216], South-Africa [217], Great-Barrier, Australia [218–220], Mediterranean Sea [221]).

Large fluctuations in settlement rates have been observed in those locations, suggesting that larval supply is episodic and spatially heterogeneous. The main factors that seem to determine the intensity of settlement in a given location at a given time are: (1) reproductive periods of adults often based on temperature, lunar phase and photoperiod [216, 218, 222, 223]; (2) hydrodynamics, at all scales (from 1000s km to <10 km), which can favour retention through inshore flowing currents, stable eddies and low flow zones or favour dispersal through offshore flowing currents (reviewed in [224]); (3) suitability

of the pelagic habitat, including predation pressure that may drastically reduce the larval pool [225, 226]; and (4) larval behaviour, as fish larvae can sense their environment and use several cues to select a settlement site and time [17, 227–229].

In the NW Mediterranean Sea, reproduction of adult fishes is typically seasonal and occurs during the spring-summer stratification period for most species, coinciding with low plankton abundance in surface layers but high phytoplankton and zooplankton biomasses at the Deep Chlorophyll Maximum [152]. In oceanic environments, offshore, the succession of assemblages starts with high abundances and low species richness in late-spring followed by lower abundances along with higher species richness in summer [180]. Post-settlement patterns (i.e. larvae that successfully settled and started their metamorphosis or already metamorphosed) have also been described for numerous species [230–233]. The intensity of settlement (evaluated with visual census of young settlers) and recruitment into juveniles were correlated in some species [230, 231, 233, 234], but not all [235]. So far, only one study quantified larval supply to coastal habitats in the Mediterranean Sea, in the South of Spain, by fishing with light-traps monthly for 13-months; Félix-Hackradt *et al.* [221]. This study highlighted some consistency in the seasonal patterns of settlement over two reproduction periods (with a one-month overlap). It also showed that diversity was highest during warmer months, from June to September, when most settlement takes place (80% of total catches). Given how variable settlement has been found to be elsewhere, the numerous factors at play in determining settlement rates and the importance of larval supply for the replenishment of coastal populations, this single, short study is not enough. It needs to be extended to be confident in the patterns observed and to understand their drivers. In addition, at all other fish larvae collection sites in the Mediterranean Sea, sampling is biased towards the new moon but the influence of the moon was never formally checked through complete systematic sampling.

The main objective of this work was to monitor, using light-traps, the larval supply of settlement-stage fish larvae to a coastal habitat of the Bay of Villefranche-sur-Mer. Sampling was conducted on a weekly basis, independently from the moon phase. We report the first three years of data to describe settlement patterns of various fish species in this site, which provide the first description of settlement patterns in this location. Additionally, we investigated the effect of several environmental variables (salinity, temperature, moonlight intensity, chlorophyll *a* concentration, and zooplankton concentrations) on larval supply rates.

4.2 MATERIALS AND METHODS

4.2.1 *Study site*

The study was conducted in the Bay of Villefranche-sur-Mer, in the Ligurian Sea, France. The bay is renowned for hosting both coastal and pelagic plankton communities close to the shore because the continental shelf is very narrow [236]. Phytoplankton concentration is controlled by zooplankton grazing during spring and autumn blooms and displays strong inter-annual variability driven by the intensity of the water column mixing during winter [192]. In the inner part of the bay, rocky areas alternate with large seagrass meadows that are potential nursery areas for several species in the Mediterranean Sea [231, 233, 234, 237, 238]. As highlighted in Chapter 2, the main hydrological structure in the region is the Liguro-Provençal current, which flows along the coast, towards the SW, at 25-35 cm s⁻¹ on average [174].

4.2.2 *Fish larvae collection*

Settlement-stage fish larvae (hereafter referred as *fish larvae*) were collected with CARE light-traps (Figure 4.2, [239]), which are the most adapted tool to sample fish larvae in the Mediterranean Sea [213]. They are also the *de facto* standard in the region because they are used in all other fish larvae collection sites.

Samples were collected weekly, usually on the night between Tuesday and Wednesday, and data were analysed for three years, from October 2012 to October 2015. The lights were turned on one hour before sunset and the light-traps were retrieved within one hour after sunrise. Two periods were sampled at higher temporal resolution to explore finer scale patterns: from May to August 2014 light-traps were set at least four days a week to describe month-scale dynamics; from July 21st to 28th (i.e. seven nights before the new moon) traps were retrieved every 40 min throughout the night to explore within-night patterns.

Light-traps were set at three sites in the Bay of Villefranche-sur-Mer which were pooled together in order to smooth local variability (Figure 4.1): (1) an inshore site (point 1) over seagrass beds at 20 m depth and located 120 m from the shore, (2) an intermediate site (point 2) over mixed rocky and seagrass bottoms at 30 m depth and also located 120 m from the shore and (3) an outer site (point 3) over 110 m depth and located at 450 m from the shore. Not all locations were sampled throughout the whole time series. Starting on October 24th 2012, only one trap was set at point 2. On June 18th 2013 a new trap

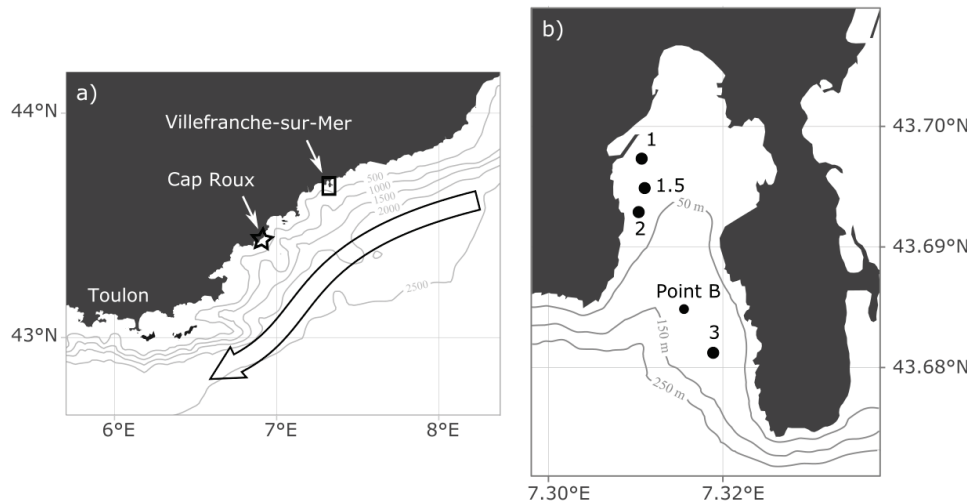


Figure 4.1: **a) Location of the Bay of Villefranche-sur-Mer (black rectangle) in the NW Mediterranean Sea.** The average position and direction of the Liguro-Provençal current are represented by the large arrow. Grey lines are isobaths (labels in metres). The closest fishing-regulated zone, “Cap Roux”, is located 40 km away. Toulon is the second largest city after Nice, the main city nearby Villefranche-sur-Mer. **b) Location of sampling sites (1, 1.5, 2 and 3) and Point B where hydrology and plankton abundances are recorded weekly.** Grey lines are isobaths (labels in metres).

was added at point 1. On September 20th 2013, a third location was added between point 1 and 2 (point 1.5) and moved to point 3 on April 24th 2014, as soon as a mooring became available at this deeper site. Since that date, all three points have been sampled as systematically as weather permitted.

Fish larvae were stored in 30 L buckets after collection, then sorted into 200 mL boxes and frozen at -24°C , with a minimal amount of water for the temperature to drop fast. Each specimen was identified under a stereomicroscope to the lowest taxonomical level (usually species) based on the available literature [154, 156, 157]. When species could not be identified, morphological groups were created; these morphological groups were denominated Genus sp1, Genus sp2, etc.

CARE light-traps exploit the inclination of settlement-stage larvae of demersal species to settle on a substrate (in this case, the net; Figure 4.2); they are therefore quite selective [239]. Still, they occasionally caught fish larvae in the pre-flexion or flexion stages as well as larvae, juveniles and young adults of strictly pelagic species, belonging to the families Belonidae, Carangidae, Centrolophidae, Clupeidae, Engraulidae, Myctophidae and Scombridae. Their occurrences are reported but all analyses focus on settlement-stage larvae of demersal species only.

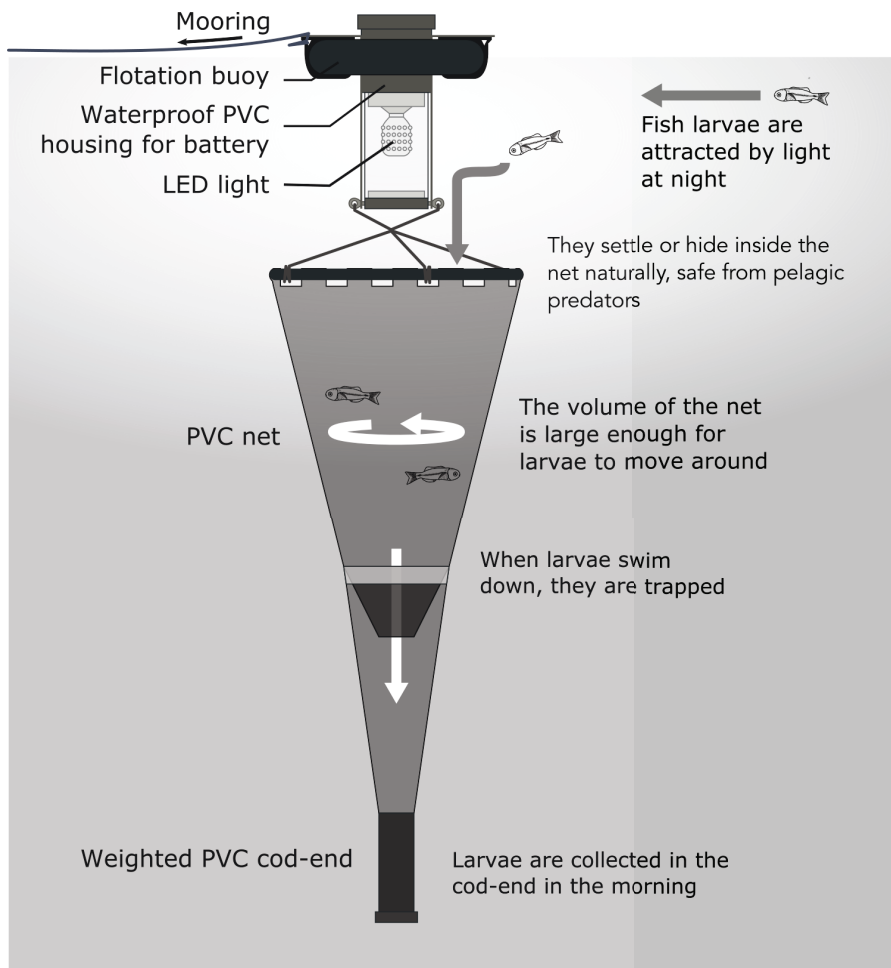


Figure 4.2: Drawing explaining the operating principle of CARE light-traps.

4.2.3 *Environmental data*

The moon phase and illumination at midnight were computed for each sampling night using the longitude and latitude of the bay, the date and the formula by Meeus [240].

Weekly records of temperature, salinity, oxygen and chlorophyll *a* concentration were made available in the Bay of Villefranche-sur-Mer over the three years of the time series by the “Service d’Observation en Milieu Littoral, INSU-CNRS” (www.somlit.fr). CTD casts and water samples were taken every Tuesday at Point B (43°10.10 N, 7°18.94 E; Figure 4.1). The raw data showcases (Figure 4.3) the marked seasonality of the region: low temperature and salinity during winter, higher salinity and temperature during summer and autumn and an early spring bloom of phytoplankton often well defined (but not in 2015). To detect the potential influence of local conditions on spawning or very early larval stages, those raw variables were used to compute the same data lagged by one month, which is the average duration of the larval phase of demersal species in the region [232, 241]. For example, if the crossing of a specific temperature threshold triggered spawning, a one-month lag would be expected between the initial environmental signal and the corresponding settlement signal.

Zooplankton was sampled with WP2 nets, twice per weekday over the whole 3-year period to capture short-term variability. Zooplankton samples were then pooled by week and classified into 66 taxonomic groups. Concentrations (in individuals per m³) were provided by the observation programme RADEZOO (www.obs-vlfr.fr).

4.2.4 *Data analysis*

The number of light-traps changed at the beginning of the study; the frequency of sampling also changed (from weekly to daily and even almost hourly). In order to compare larval settlement rates between periods, abundances were standardized to Catch Per Unit of Effort (CPUE); “effort” being both time fished and number of traps. CPUE is often used as a proxy of the abundance of settlement-stage fish larvae [e.g. 217, 219, 221]. For the year scale, all data were considered and CPUE was computed as the average number of larvae per light-trap per night to result in one value per week. The month scale was investigated from the four-nights-a-week sampling in 2014; CPUE was still the average number of larvae per light-trap per night but with one value per day. To determine the abundances during the seven nights sampled at high frequency in July 2014, we calculated CPUE as the number of larvae per trap per 40 min.

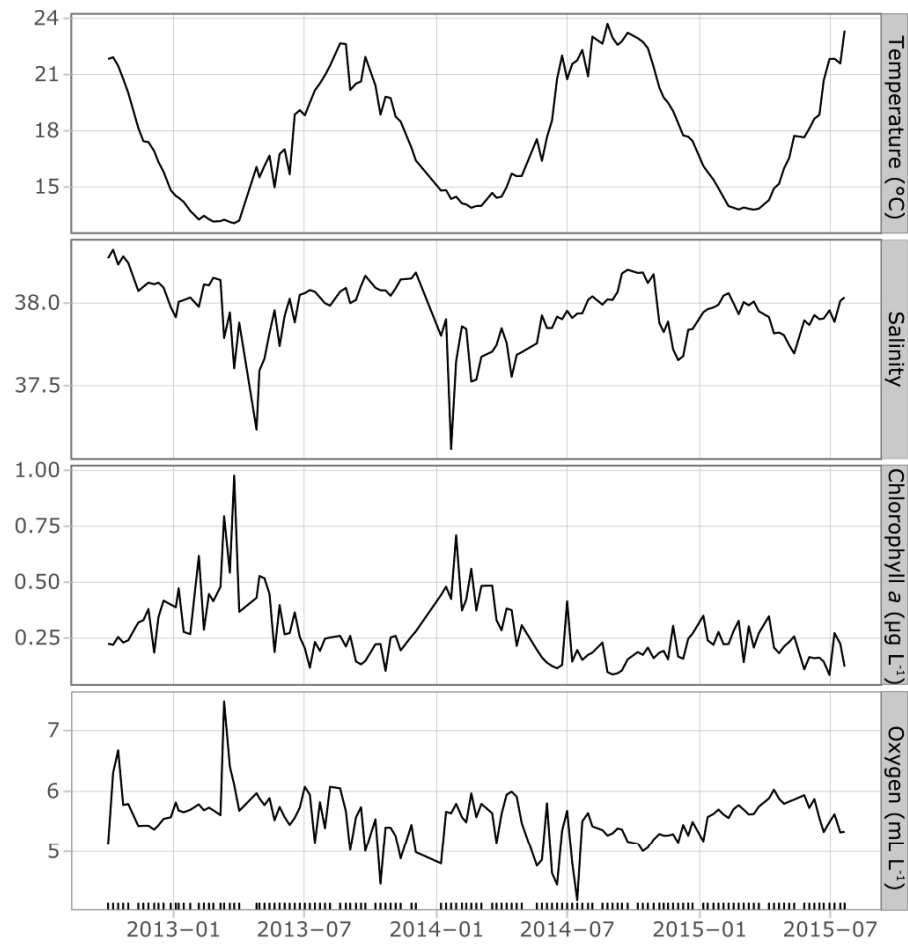


Figure 4.3: Hydrology throughout the sampling period, denoting the marked seasonality of the region. Dashes along the x-axis mark sampling dates.

Despite best efforts, there were some missing values in the weekly time series of hydrology, zooplankton and fish larvae settlement. Missing values were filled through linear interpolation to obtain complete, regular, weekly time series. Weighted moving averages with a one-month window were used to smooth-out instantaneous variability and highlight longer scale patterns, in particular seasonal ones.

The relative timing of the phytoplankton bloom, the zooplankton bloom and the peak of larval fish settlement was explored through cross-correlation of the regularised time series of chlorophyll *a*, concentration of copepods ($\log(n+1)$ transformed) and total CPUE of fish larvae, pooled across species (also $\log(n+1)$ transformed).

The influence of the environment (hydrology, moon phase and abundance of other zooplankton groups) on the composition of larval assemblages was explored through a Constrained Canonical Analysis (CCA). Only the potential prey of fish larvae (copepods [242]: *Oithona* spp, *Candacia* spp, *Acartia* spp, small copepods and nauplii; appendicularians [165]) or their predators (chaetognaths [166]; *Pelagia noctiluca* ephyrae [167]) were selected for the analysis among the 66 available groups of zooplankton. Influential variables were selected with an automatic stepwise procedure designed for constrained ordination methods [243].

The relationship between CPUE per species and environmental variables was tested through Generalized Linear Model (GLM) for the 12 most abundant species, each of which represented >1% of total catches. An over-dispersed Poisson distribution was assumed for CPUE.

Settlement occurred in pulses for the six most abundant species. This was particularly noticeable during the four months of intense sampling in spring-summer 2014. Pulse intensity was quantified with an index of temporal aggregation: the number of nights necessary to accumulate >50 % of the catches of the four months. In addition, pairwise Wilcoxon tests were applied to detect significant differences in settlement intensity among the four quarters of the moon cycle (Q1: new moon to first quarter, Q2: first quarter to full moon, Q3: full moon to third quarter and Q4: third quarter to new moon).

All analyses were conducted with R (3.1.2) [171] with packages *plyr* (1.8.1) and *dplyr* (0.4.1) for data manipulation, *ggplot2* (1.0.1) for plotting, *vegan* (2.2.0) for CCA, *oce* (0.9.14) for moon phase calculations and *pastecs* (1.3.18) for time series analyses.

4.3 RESULTS

4.3.1 *Fish assemblages*

A total of 2527 settlement-stage fish larvae of demersal species were caught over 212 nights, which amounts to 4.35 fish larvae per trap per night fished. In terms of diversity, the catches spanned 16 families, 26 genera and 46 species, although only seven families had more than ten individuals (Table 4.1). The four most abundant species were all Sparidae: *Diplodus annularis*, 13.1%; *Spicara smaris*, 12.4%; *Sarpa salpa*, 10.9%; and *Pagellus bogaraveo*, 10.9%. This family represented 59.4% of the total CPUE, followed by Blenniidae (12.5%), Pomacentridae (10.6%; a single species of this family is present in the Mediterranean Sea, *Chromis chromis*) and Mugilidae (5.9%). Every other family represented less than 3% of the catches.

Table 4.1: Complete report of catches. Only settlement-stage larvae of demersal species are considered in the rest of the study.

Family				
Species	2012	2013	2014	2015
Fishes				
Ammodytidae				
<i>Gymnammodytes spp</i>		2	2	2
Apogonidae				
<i>Apogon imberbis</i> (Linnaeus, 1758)		1	1	
Atherinidae				
<i>Atherina boyeri</i> Risso, 1810		11	3	2
<i>Atherina hepsetus</i> Linnaeus, 1758		3		
<i>Atherina spp</i>				4
Belonidae				
<i>Belone belone</i> (Linnaeus, 1761)			2	
Blenniidae				
<i>Lipophrys trigloides</i> (Valenciennes, 1836)			32	
<i>Parablennius spp</i>	1	30	105	20
<i>Parablennius gattorugine</i> (Linnaeus, 1758)			2	
<i>Parablennius incognitus</i> (Bath, 1968)			15	6
<i>Parablennius pilicornis</i> (Cuvier, 1829)			5	
<i>Parablennius rouxi</i> (Cocco, 1833)		1	17	2
<i>Parablennius tentacularis</i> (Brünnich, 1768)			3	
<i>Parablennius zvonimiri</i> (Kolombatovic, 1892)			7	
<i>Salaria pavo</i> (Risso, 1810)			2	
Bothidae				

(continued)

Table 4.1: (continued)

Family	Species	2012	2013	2014	2015
	<i>Arnoglossus spp</i>			1	
Carangidae					
	<i>Seriola dumerili</i> (Risso, 1810)				1
	<i>Trachurus spp</i>			100	12
Centrolophidae					
	<i>Schedophilus ovalis</i> (Cuvier, 1833)			2	
Clupeidae					
	<i>Sardina pilchardus</i> (Walbaum, 1792)		1	74	56
Congridae					
	<i>Conger conger</i> (Linnaeus, 1758)			1	6
Engraulidae					
	<i>Engraulis encrasicolus</i> (Linnaeus, 1758)	1	86	25	536
Gadidae					
	<i>Gaidropsarus mediterraneus</i> (Linnaeus, 1758)		2	17	
	<i>Micromesistius poutassou</i> (Risso, 1827)		1		
	Unidentified		2	1	
Mugilidae					
	Mugilidae <i>sp1</i>		9	12	13
	Mugilidae <i>sp2</i>			2	
	Mugilidae <i>sp3</i>			2	1
	Mugilidae <i>sp4</i>			4	2
Mullidae					
	<i>Mullus barbatus</i> Linnaeus, 1758			1	
	<i>Mullus surmuletus</i> Linnaeus, 1758			1	1
Myctophidae			1	2	1
Pomacentridae					
	<i>Chromis chromis</i> (Linnaeus, 1758)		11	85	80
Sciaenidae					
	<i>Sciaena umbra</i> Linnaeus, 1758				1
Scombridae					1
Scorpaenidae					
	<i>Scorpaena porcus</i> Linnaeus, 1758		2	15	
	<i>Scorpaena scrofa</i> Linnaeus, 1758			6	
Serranidae					
	<i>Epinephelus marginatus</i> (Lowe, 1834)			2	
	<i>Serranus hepatus</i> (Linnaeus, 1758)			2	
Sparidae					
	<i>Boops boops</i> (Linnaeus, 1758)		5	341	
	<i>Dentex dentex</i> (Linnaeus, 1758)			1	

(continued)

Table 4.1: (continued)

Family		2012	2013	2014	2015
	<i>Species</i>				
	<i>Diplodus annularis</i> (Linnaeus, 1758)		38	371	83
	<i>Diplodus puntazzo</i> (Walbaum, 1792)	1	8	13	2
	<i>Diplodus sargus</i> (Linnaeus, 1758)		1	8	1
	<i>Lithognathus mormyrus</i> (Linnaeus, 1758)	1	2	3	
	<i>Oblada melanura</i> (Linnaeus, 1758)		31	307	4
	<i>Pagellus acarne</i> (Risso, 1827)		1	1	
	<i>Pagellus bogaraveo</i> (Brünnich, 1768)	26	18	21	15
	<i>Pagellus erythrinus</i> (Linnaeus, 1758)			2	
	<i>Pagrus pagrus</i> (Linnaeus, 1758)			5	3
	<i>Sarpa salpa</i> (Linnaeus, 1758)	23	7	48	8
	<i>Spicara smaris</i> (Linnaeus, 1758)		5	505	4
	<i>SpondylIOSoma cantharus</i> (Linnaeus, 1758)			12	2
	Unidentified		2	38	3
Syngnathidae					
	<i>Hippocampus hippocampus</i> (Linnaeus, 1758)			1	1
Triglidae					
	<i>Chelidonichthys lucerna</i> (Linnaeus, 1758)			1	2
Uranoscopidae					
	<i>Uranoscopus scaber</i> (Linnaeus, 1758)			1	
Unidentified and others					
	Unidentifiable		5	5	1
	Octopodidae				1
	Sepiolidae		1	2	3
Total		52	286	2222	900
Sampling effort					
	<i>nights x number of light-traps</i>	8	83	316	147

4.3.2 Year-scale dynamics

Seasonal patterns were consistent between years, with a main abundance peak in late spring - early summer, from April to July (66.7% of catches were in this period) and a second, weaker one, in autumn, from October to December (20.5% of catches; Figure 4.4). Abundances were very low throughout winter, from January to March, but also quite low in late summer, from mid-August to September (Figure 4.4).

Cross-correlation revealed a quite consistent and strongly significant succession: the peak of chlorophyll *a* was followed 5 weeks later by a peak in the concentration of copepods which itself was followed 12 weeks later by a peak in CPUE of fish larvae (Figure 4.5). This was

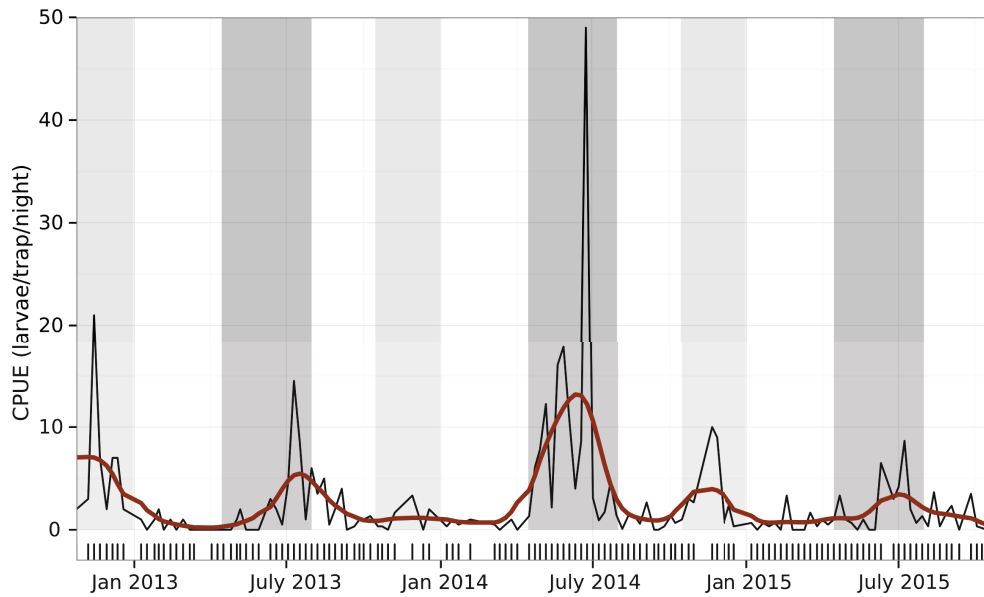


Figure 4.4: **CPUE of settlement-stage fish larvae of demersal species throughout the sampling period.** Dashes along the x-axis mark sampled weeks. The thin line is the raw data. The thick line is a one-month moving average. The main settlement periods are highlighted: late spring-early summer (dark grey) and autumn (light grey).

true both for the spring bloom and the autumn bloom. Even though the timing of the peaks matched, the intensity of larval fish supply to the bay did not reflect the intensity of the phytoplankton or zooplankton blooms. Indeed, the highest larval fish abundances were in 2014, a year of intermediate bloom intensity (Figure 4.5).

Taxonomic richness peaked to >20 taxa in early summer (June-July), during and after the period of high abundance and remained below 8 taxa for most of the rest of the year (Figure 4.6). Most taxa were collected over a time span of one to two months (e.g. *Gaidropsarus mediterraneus* and *Chelidonichthys lucerna* in early spring, or *C. chromis*, *Mugilidae sp1* and *Scorpaena porcus* in late summer; Figure 4.6). Sparidae were collected throughout the year and displayed a consistent succession of species (Figure 4.6). *Boops boops* was the first sparid observed in spring, followed by *Diplodus sargus*, *Pagellus acarne*, *S. smaris*, *Spondyllosoma cantharus*, *Dentex dentex* and *Pagrus pagrus*. In early summer, *D. annularis* was closely followed by *O. melanura* and other species of the genus *Pagellus*. *Diplodus puntazzo* was observed over a very short period in autumn, with high consistency among years. Finally, *S. salpa* and *P. bogaraveo* were recorded throughout winter, yet in higher abundance before January (Figure 4.6).

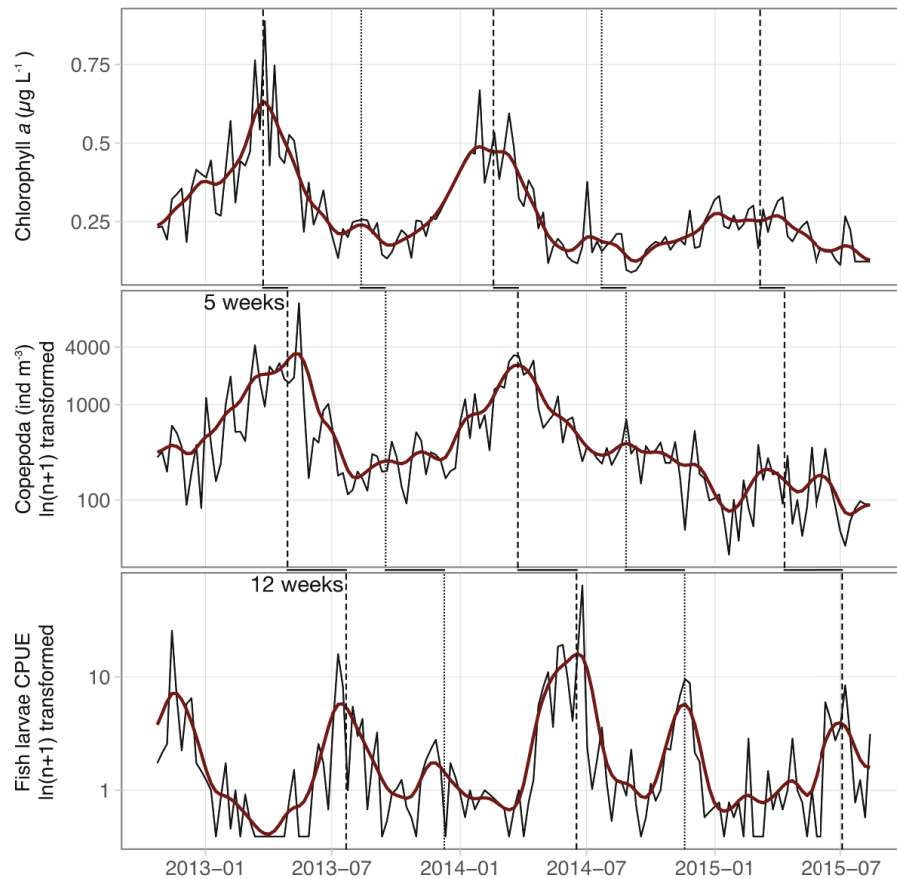


Figure 4.5: **Ecological succession through three trophic levels.** The thin lines are the time series regularised on a one-week time step. The thick lines are a one-month moving average. The vertical dashed lines highlight the spring phytoplankton bloom and the related succession. The vertical dotted lines highlight the autumn bloom and succession.

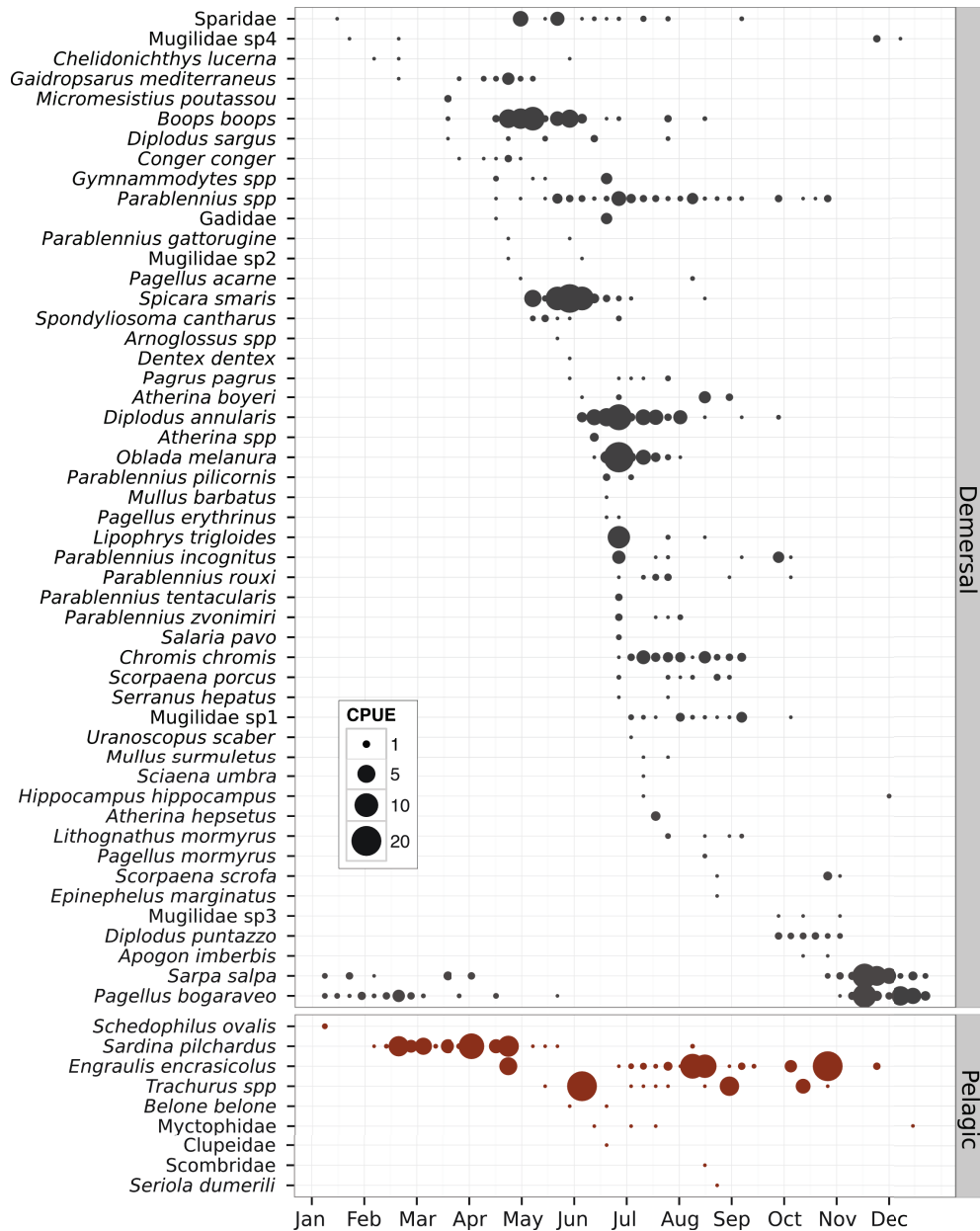


Figure 4.6: Abundances of all taxa throughout the year (averaged over all years sampled). Taxa are ordered according to the date of their first occurrence. Dot size is proportional to CPUE. Pelagic taxa are represented for completeness (bottom panel) but all analyses focus on settlement-stage larvae of demersal fish taxa only (top panel).

The composition of larval fish assemblages was strongly seasonal too: only season, temperature, salinity and their one-month lagged versions (i.e. the environmental variables with the strongest seasonal signal) were selected in the parsimonious CCA. The model was highly significant and environmental variables explained 29.2 % of inertia ($p < 0.001$; Figure 4.7). All 19 other potential explanatory variables were discarded: abundances of all zooplankton taxa, moon illumination, year, but also oxygen and chlorophyll *a* as well as their lagged versions. Five assemblages were differentiated (Figure 4.7). *Diplodus puntazzo*, *Apogon imberbis*, *Scorpaena scrofa* and Mugilidae *sp3* constituted an autumn assemblage and were related to the highest salinity levels (both raw and one-month lagged) and high water temperature in the previous month (Figure 4.7). Winter species (*P. bogaraveo*, *S. sarpa* and Mugilidae *sp4*) were well separated from all others and not related to any hydrological variable. Four species composed a winter-spring transition assemblage, occurring together at lowest temperature levels (*C. lucerna*, *G. mediterraneus*, *Conger conger* and *B. boops*). The species of the spring assemblage were associated with low salinity levels, both during and one month before their occurrence, but also to low temperatures the month before (Figure 4.7). *Dentex dentex* and *SpondylIOSoma cantharus*, two highly valuable species for fisheries, were collected during this period. Finally, the summer assemblage could be related to increasing seawater temperature (Figure 4.7). This assemblage displayed the highest diversity, including larvae of emblematic species, such as *Hippocampus hippocampus* and *Epinephelus marginatus*.

The regressions of the abundance of any single species with each environmental variable and its lagged version were never significant (GLM, all p -value > 0.05).

Average CPUE was higher in 2012 and 2014 (6.4 and 6.4 larvae per trap per night respectively) compared to 2013 and 2015 (2.0 and 1.9 respectively). In addition, all summer species arrived on average 19 days earlier in 2014 compared to the other years, while autumn species arrived at the same period over the three years (Figure 4.3). The early arrival may be related to the fact that, in spring 2014, surface water temperature started rising four weeks earlier compared to 2013 and 2015 (Figure 4.3). Finally, species richness was two times higher in 2014 (42 morphospecies) compared to 2013 and 2015 (22 and 26 morphospecies); but sampling effort was much higher that year (108 nights sampled in 2014 versus 47 in 2013, 49 in 2015¹).

¹ Only eight nights were sampled in 2012, which resulted in very low species richness (5 species)

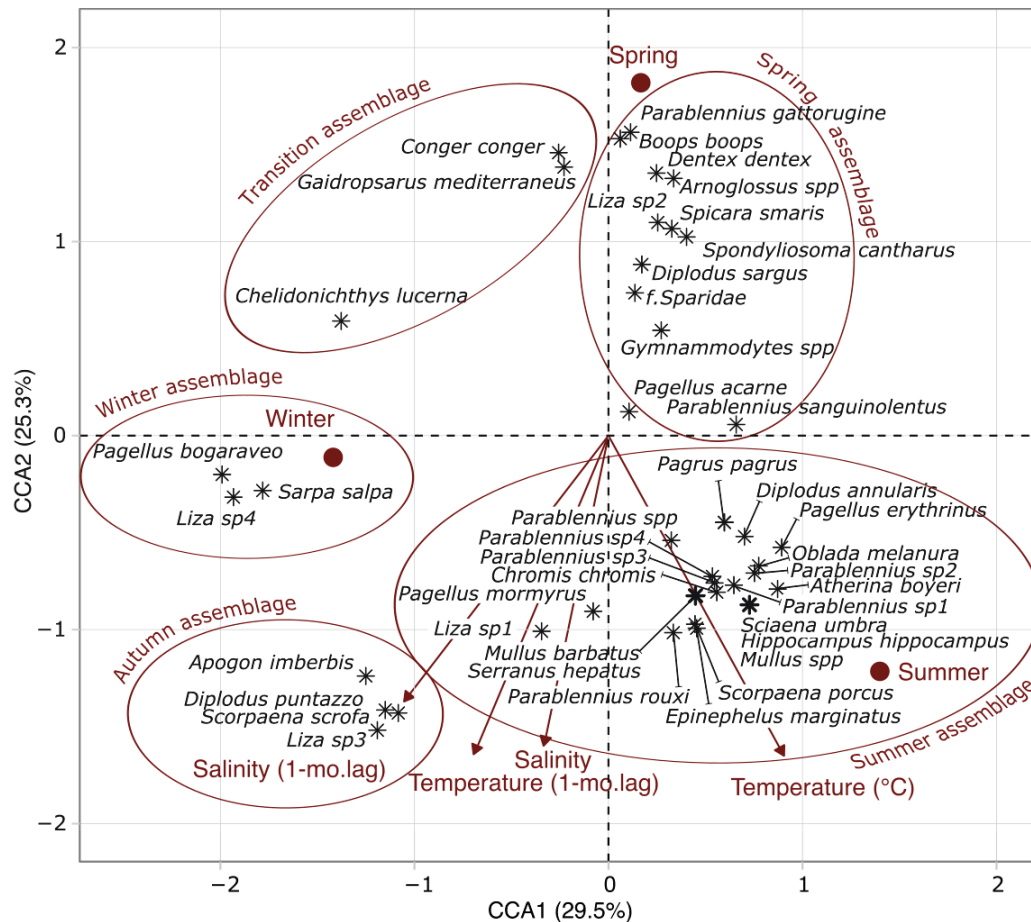


Figure 4.7: **Biplot for the constrained correspondence analysis (CCA) relating larval fish assemblages to hydrological variables and season.** Species located around the tip of a variable vector had larger relative abundance at high values of the variable (and conversely, species located opposite to a variable vector had larger relative abundance at *low* values of the variable). Species located around a season marker were more abundant during this season (with qualitative variables in CCA, one level is taken as a reference to which others are compared; the reference level, here autumn for the season variable, is not represented in the CCA space). Environmental variables significantly explained 29.2% of the total inertia ($p < 0.001$). The percentages are the proportion of inertia explained by each axis. Thicker dots indicate that at least two species share the same coordinates in the first two axes of the CCA space.

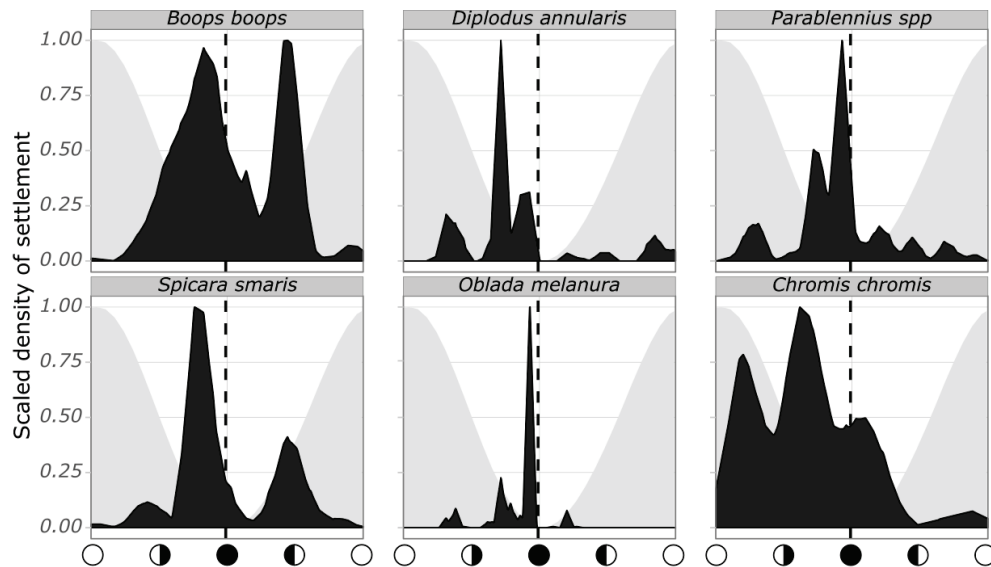


Figure 4.8: Density of settlers of the six most abundant species over a lunar month. The light grey area is the moon illumination curve. The phases of the moon are represented on the x-axis. The density of settlers is scaled to a maximum of one in all plots to ease comparison.

4.3.3 Month-scale dynamics

During the intense sampling period of 2014, fish larvae settled in higher proportions between the last quarter and the new moon (Q4) compared to other quarters (significantly with Q2 and Q3, Pairwise Wilcoxon test, both p -value <0.05 , and almost significantly with Q1, right after the new moon, Pairwise Wilcoxon test, p -value=0.06). Indeed, 63.3% of fish larvae were collected during Q4, while only 19% were captured during Q1 and less than 10% during both Q2 and Q3. *Boops boops* recruited over the widest period within the lunar month and had the lowest temporal aggregation index within the Sparidae (four nights; Figure 4.8). *Oblada melanura*, *D. annularis* and *S. smaris* were more aggregated, mostly within Q4, and 50 % of the larvae of *O. melanura* settled on the night before the new moon. The temporal aggregation index was two nights for *D. annularis* and *S. smaris* (Figure 4.8). *Parablennius spp* and *C. chromis* also exhibited strong peaks before and on the night of the new moon; yet they were also recorded in low abundance over a wider period, as indicated by the higher values of aggregation index (6 and 5 nights respectively).

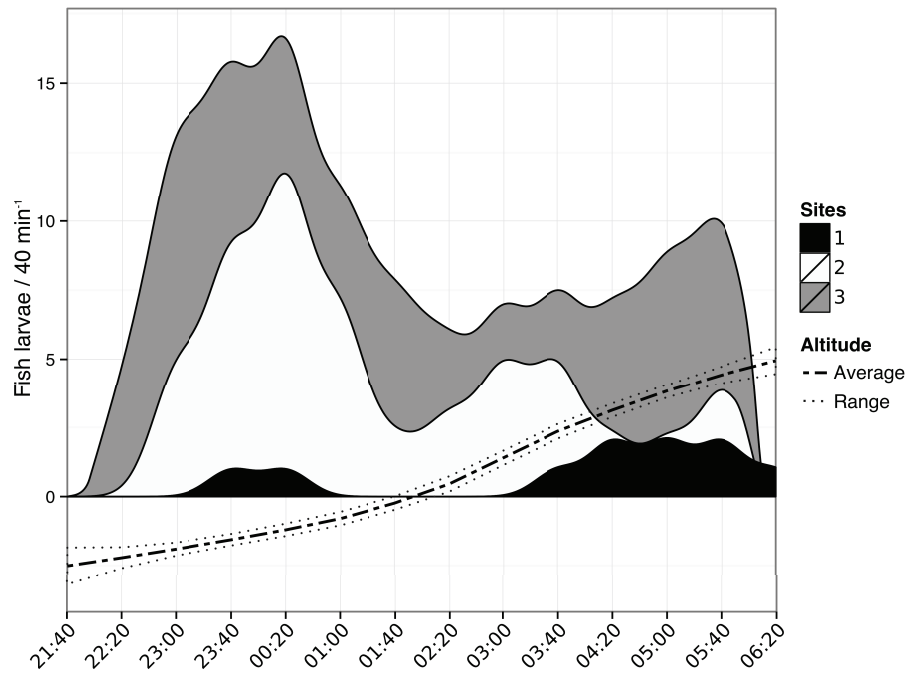


Figure 4.9: Larval fish counts over 40 min bins throughout the night, stacked per sampling site. Counts were smoothed by a kernel method. Dashed lines indicate the mean elevation of the moon and its range throughout the week (in degrees from the horizon, scaled by a factor of 0.1). The moon rose when elevation crossed 0 (at about 01:40).

4.3.4 Night-scale dynamics

Only 125 settlement-stage larvae were collected over the 7 nights sampled at high frequency (5.95 larvae/trap/night), which was considerably fewer than during previous new moons periods (Figure 4.4). Still, patterns could be detected. Fish larvae were very scarce at dusk and dawn, while maximum abundances were observed three hours after sunset, before the moon rose (Figure 4.9). After this peak, very few larvae settled, although some were systematically collected about one hour before dawn (Figure 4.9). During the first, main peak, fish larvae were caught first at the entrance of the bay (site 3; Figure 4.9), then at the intermediate site (site 2) and finally at the most inshore location (site 1).

4.4 DISCUSSION

4.4.1 Selectivity of light-traps

All collected fish taxa were reported and very few could not be identified to species. However, it must be kept in mind that light-traps

are selective and sample only positively phototactic larvae [215]. This may lead to a taxonomic bias and possibly lower sampling efficiency of some species compared to other methods [244]. For example, Labridae display a complex phototaxis behaviour [245] and their abundance is clearly underestimated by light-traps [246]. Labridae are observed in the Bay of Villefranche-sur-Mer and in the region [247]; larval stages can be collected in the bay using plankton nets (*pers. data*). The fact that not a single specimen of Labridae was collected in light-traps is evidence of their selectivity. Nevertheless, comparisons between studies are likely to be relevant, as this bias seems to be the same in different locations (e.g. Australia [215]; Florida [216, 246]; Caribbean [248]; Mediterranean Sea [221]). Despite this bias, light-traps remain the best sampling gear to quantify the abundance of settlement-stage larvae in the Mediterranean Sea [213].

4.4.2 *Year-scale patterns of larval supply and relationships with environmental conditions*

Immediate hydrological conditions at the time of settlement or one month before did not influence the settlement rate of any species. This is not surprising because settlement is the result of longer and larger scale processes spanning the whole larval phase, which may be decorrelated from local changes in environmental conditions at the future settlement site. Over longer scales, this time series highlighted the consistency of seasonal patterns in the abundance and assemblages of fish larvae throughout the years. It also pointed out differences in the timing of the spring/summer peak of larval supply to the area among the years. Those differences are very likely linked to changes in the timing of the spring blooms of phyto- and zooplankton (Figure 4.5). Indeed, the lag between the blooms and the peak of larval supply was very consistent (Figure 4.5) and the late blooms in 2013 and 2015 led to a delay in the arrival of the first individuals of the year as well as in the following abundance peak. However, the fluctuations in the *intensity* of larval supply among years did not seem related to the intensity of the phytoplankton and zooplankton blooms, supporting that prey abundance may not be a limiting factor for larval fish settlement in the Bay of Villefranche-sur-Mer. Contrastingly, the autumn peak showed very low among-years variations in both timing and intensity. These observations support the idea that, while species-specific settlement is not related to local conditions, the broad settlement patterns are influenced by environmental conditions at the seasonal scale [15, 152].

The most abundant family in the catches, the Sparidae, have a pelagic larval duration ranging from ~2 to 5 weeks depending on the spe-

cies [232]. Thus, according to the “Match-mismatch” hypothesis [20], the 12-week lag between the main peak of zooplankton abundance and larval fish settlement reveals a considerable temporal mismatch between the two. Nevertheless, settlement patterns were consistent over the years, suggesting that the spawning period of adults (therefore the period at which fish larvae are present in the ocean) is forced by other processes. One explanation for this mismatch might be that the zooplankton bloom period, despite the abundance of prey, is actually unfavourable to fish larvae due to low temperatures and sometimes enormous abundances of gelatinous organisms (e.g. salps, ctenophores, medusae; RADEZOO and *pers. obs.*) that would consume a large proportion of the available prey and predate on fish eggs and larvae. Thus, although the period of higher fish settlement consistently related to the timing of the phytoplankton and zooplankton blooms, the intensity of settlement seems driven by other, still unknown factors.

4.4.3 Comparison with previous studies

The temporal patterns of settlement observed were consistent with the spawning period of Mediterranean fishes: most settlement-stage larvae were caught within one to two months of their reported spawning period in the NW Mediterranean Sea or Adriatic Sea (e.g. *Spicara smaris* in April-May, *B. boops* in March to June, *D. puntazzo* from August to October, *S. sarpa* in September-October; [223]). The general patterns of settlement also concurred with previous studies conducted in the NW Mediterranean Sea. Although those were more limited in time, they also detected higher abundances and diversity during the warmer months [221] and a decrease in abundance concurrent with an increase in species richness throughout summer [180]. The addition of this longer-term study, in a new location, suggests that these temporal patterns seem consistent between years and geographically, over the NW Mediterranean Sea.

Taxonomic diversity was similar between this study (46 taxa) and that of Félix-Hackradt *et al.* [221] conducted in the south of Spain in 2010-2011 (42 taxa when removing the non-target ones), although the Spanish study targeted a network of Marine Protected Areas, where diversity could be expected to be higher [249]. Still, average abundances were lower in the Bay of Villefranche-sur-Mer compared to Félix-Hackradt *et al.* [221] (4.35 larvae/trap/night versus 7 larvae/trap/night).

Another inconsistency is that Félix-Hackradt *et al.* [221] found high abundances of fish larvae from June to September while, in this study, the period of high abundance was May-June and larvae were always

scarce in August and September. However, they included Carangidae and Clupeidae as target taxa while we did not; those taxa were among the most abundant and peaked in August and September, likely explaining the discrepancy.

In addition, Félix-Hackradt *et al.* [221] could only sample on the nights of the first and third quarters of the moon due to logistical limitations and concluded that moon illumination had a very limited influence on the settlement of fish larvae. Here, with a more systematic and intensive sampling strategy, a marked influence of the moon on settlement was detected. The contrasting results between these two studies suggest that future studies aimed at quantifying larval supply in the Mediterranean Sea should be set up according to the moon cycle and that sampling effort should be focused on moonless nights.

4.4.4 *Predation avoidance and gregarious behaviour*

The influence of the moon on adult spawning is well documented in the tropics [222, 250, 251] and most larvae settle between the third quarter and the new moon [216, 219, 248]. The present study highlighted the same pattern in this location of the Mediterranean Sea, as the vast majority of the catches occurred around the new moon, in particular between the third quarter and the new moon. Furthermore, even if the results should be taken with caution due to the low number of fish larvae collected, the night-scale monitoring suggested that fish larvae settled mostly during the moonless hours of the night (even just before the new moon, when moon illumination was very low anyway). So overall, fish larvae seemed to settle in higher numbers when the night was darkest. Settling fish larvae are strongly predated upon by adult coastal fishes [30, 226, 252, 253], which are visual predators. This pattern of settlement may therefore have evolved as a predation-avoidance mechanism, involving both the timing of spawning by the adults (which then puts settlement around the new moon) and probably finer scale adjustments by larvae themselves, in particular to target the moonless hours of the night.

Light-traps cannot be used to monitor settlement during the day, obviously. If larvae also settled during the day, the previous hypothesis would be invalidated. In the tropics, settlement of fish larvae was suggested to be limited to the night by monitoring using crests-nets [227] and plankton nets [254] as well as behavioural observations *in situ* [253]. Unfortunately, no data is available for the species captured here.

The synchronicity with the lunar cycle could also be related tides and in particular to tidal currents that may transport fish larvae in-

shore [216]. However, this explanation is not likely to apply in the NW Mediterranean Sea where tides are negligible [255].

Larval supply has almost always been found to be very variable at small spatial and temporal scales [e.g. 216, 219, 221]. It was also highly variable in this study, both between sites (spatial scale <1 km) and between nights (temporal scale <24 h), while environmental conditions were similar at those scales. For the most abundant species, the difference in catches between sites or between two consecutive nights often reached 50-fold, but the species that arrived in such pulses have different spawning strategies: *S. smaris* spawns benthic eggs while the others spawn pelagic eggs. So the initial cohesion of the larval fish pool may not be related to those pulses. Furthermore, larvae of benthic-spawning species may actually be transported as far offshore as those of pelagic spawners [Chapter 2; 256].

Finally, for the species studied here, settlement-stage fish larvae of benthic or pelagic spawners are similar morphologically (transparent, elongated body) and have comparable behavioural abilities (to be explored in Chapters 5 and 6). These pulses may thus be the result of gregarious behaviour at the end of the pelagic phase, as is commonly observed for barnacles (crustaceans [224]) and was suggested for fish larvae [e.g. 216, 219, 227]. Indeed, it has been observed in pelagic stages of Gobiidae and Mugilidae, above 6 mm [257, 258], and during or after settlement in Pomacentridae, Mullidae, Lutjanidae and Microdesmidae [253, 259]. Otoliths microchemistry also suggests that fish larvae from different cohorts may aggregate very early in their pelagic phase and remain grouped until reaching their settlement habitat [260]. The processes enabling such aggregations in the open ocean remain unclear. It has been hypothesised that some patches may be created soon after hatching or by gathering into patches of high food concentration such as convergence zones [261]. Then, remaining as a group until settlement may be possible using vision [262] or sounds, as observed for larvae of Lutjanidae [263]. Moving in groups has many known advantages: it improves predator detection in spiny lobsters [264] and birds [265], dilutes the predation risk in adult teleost fishes [266] and enhances the orientational abilities of birds [267] and coral reef fish larvae [268].

Overall we hypothesise that settlement-stage fish larvae follow a strategy that reduces their predation risk (and may improve their behavioural abilities) by settling in groups, preferentially during the moonless hours of nights around the new moon.

4.5 CONCLUSIONS

This study highlighted consistent, strong seasonal and lunar patterns in the settlement of fish larvae to the Bay of Villefranche-sur-Mer, in the Mediterranean Sea. These patterns are comparable to what has been observed in more details in tropical environments. The most abundant species, at least, seemed to follow a predator avoidance strategy by settling in pulses during the darkest hours of moonless nights.

Abundance and taxonomic diversity were both high although the study site is subjected to professional and recreational fishing and located more than 40 km downstream the closest marine protected area ("Cantonement du Cap Roux"). The bay of Villefranche-sur-Mer seems to receive substantial larval supply, at least comparable to other locations in the NW Mediterranean Sea. In addition, the existence of historical monitoring programs surveying hydrology and zooplankton in the bay makes it particularly suited for studying the relationship between larval fish settlement and various environmental drivers, the influence of which was suggested by the consistent ecological succession presented here. The monitoring of larval fish settlement shall therefore continue in the Bay of Villefranche-sur-Mer.

4.6 ACKNOWLEDGMENTS

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SUN-COMPASS ORIENTATION IN MEDITERRANEAN FISH LARVAE

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Modified version of the article Faillettaz et al., 2015.
Sun-Compass Orientation in Mediterranean Fish Larvae.
Plos ONE, 10(8):e0135213

5.1 INTRODUCTION

The pelagic eggs and larvae of demersal fish species can be transported over hundreds of kilometres by ocean currents [87]. Despite this potential for long distance transport, self-recruitment has been found to be consistently high (often >30% [e.g. 82, 83]). As mentioned in the introduction (Section 1.5, p. 34), the behavioural abilities of fish larvae are known to be well developed at least in tropical species and at settlement-stage: they can sense their environment, swim vertically and horizontally and orient [100]. Such behaviours are often invoked to explain how larvae can influence their dispersal and favour retention [82, 93, 269]. Vision, hearing and olfaction can be used by settlement-stage larvae to locate a coastal habitat over short distances (metres to kilometres) [117, 122, 270]. Larvae likely use different cues for orientation at various stages of development and distances to their settlement habitat [228].

Yet, it is still unclear whether fish larvae are capable of orienting in an oceanic environment where they would have only globally-available cues. Global mechanisms effective for long distance orientation include magnetic or celestial compasses [271] but there is no evidence so far regarding the existence of a magnetic compass in fish larvae. The use of a sun compass was first proposed for Clupeidae [272], then suggested for Pomacentridae larvae [273] and recently observed in laboratory experiments on Apogonidae larvae [124] and *in situ* on non-native, reared Pomacentridae larvae [274]. Consistent orientation,

through the use of a sun compass for example, could make a difference in dispersal outcome compared to passive advection [275].

While theoretical frameworks exist to include behaviour in biophysical dispersal models [88, 276, 277], empirical data are still crucially lacking [115, 228, 269]. Furthermore, most studies on larval fish orientation have been conducted in tropical and insular environments: Lizard Island [100, 116, 278] and One Tree Island [122, 124] in the Great Barrier Reef, Australia; Taiwan [16]). Only three studies looked at orientation in (warm) temperate environments [270, 279, 280] and only one was carried out along a continuous shore, although in a subtropical environment and using non-native, reared larvae [274]. This lack of diversity makes the interpretation of such observations difficult and prevents their generalisation into a set of universal orientation rules, which could be implemented in models.

The Ligurian coast (Northwestern Mediterranean Sea) notably differs from insular or tropical environments. The geomorphology is homogeneous; rocky capes alternate with sheltered bays over hundreds of kilometres, from Genova (Italy) to Toulon (France). The continental shelf is extremely narrow, never expanding more than a few hundred metres from the coastline. Settlement and adult habitats are thus constrained to near-shore areas. The Liguro-Provençal current, presented in Chapter 2, is the main oceanographic feature of the region: a strong jet which flows along the coast, between the surface and 150-200 m depth, in a southwestward direction at an average speed of 25-35 cm s⁻¹, and creates mesoscale meanders and eddies [143] (Figure 5.1). No data on larval fish behaviour exist in such an environment. Furthermore, the proximity between truly oceanic waters (bottom depth >1000 m) and the coast makes it very convenient to study the behaviour of wild-caught settlement-stage larvae in an oceanic environment.

This study used an *in situ* observation instrument to provide the first data on orientation behaviour of Mediterranean settlement-stage fish larvae. We quantified the ability of settlement-stage larvae to keep a bearing and then assessed which environmental variables may influence their orientation. We focused on sun-related variables that could drive orientation over long distances.

5.2 MATERIALS AND METHODS

5.2.1 Larvae collection and handling

Settlement-stage fish larvae (herein referred as *fish larvae*) collection was described in Chapter 4 (Section 4.2.2, p. 99). Larvae used for this

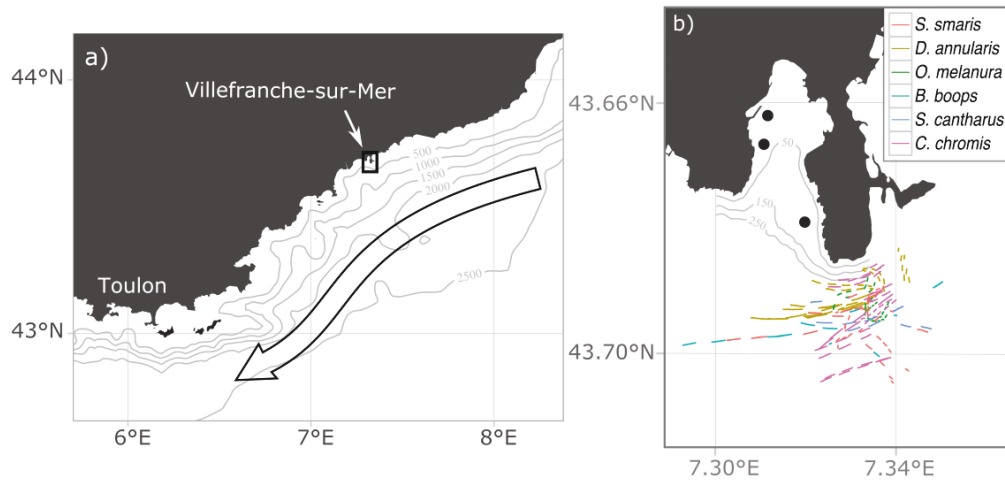


Figure 5.1: **a) General location of the study area (black rectangle) in the NW Mediterranean Sea.** The average position and direction of the Liguro-Provençal current are represented by the large arrow. Grey lines are isobaths (labels in metres). Toulon is the second largest city after Nice, the main city nearby Villefranche-sur-Mer. **b) Detailed map of collection sites and deployments.** The black dots represent collection sites of settlement-stage fish larvae, as presented in Chapter 4. Segments represent the drifting trajectories of the instrument over each 15 min deployment. Grey lines are isobaths (labels in metres).

study were collected between May and July 2014. After collecting light-traps, fish larvae were sorted visually and kept in 30 L buckets. Back in the laboratory, buckets were placed in a temperature-controlled room at 19°C (close to or slightly lower than seawater temperature measured *in situ*).

Six common species, of ecological and/or commercial interest, were chosen for the tests (Figure 5.2). *Boops boops*, *Spicara smarlis* and *Spondyllosoma cantharus* were tested between May 7 and 28; *Oblada melanura* and *Diplodus annularis* between June 23 and July 1; and *Chromis chromis* between July 16 and 27.

After a few hours in the lab, fish larvae were taken back offshore to be observed *in situ*. Ninety percent of larvae were tested on the day of capture and 99% within 48h of capture. At the end of the day, larvae were euthanised at -20°C. Within a week, specimens were defrosted, identified to species-level based on [154, 156, 157] and measured (standard length) to the closest 0.1 mm using an image capture software under a microscope (NIS Element 4.11 D).

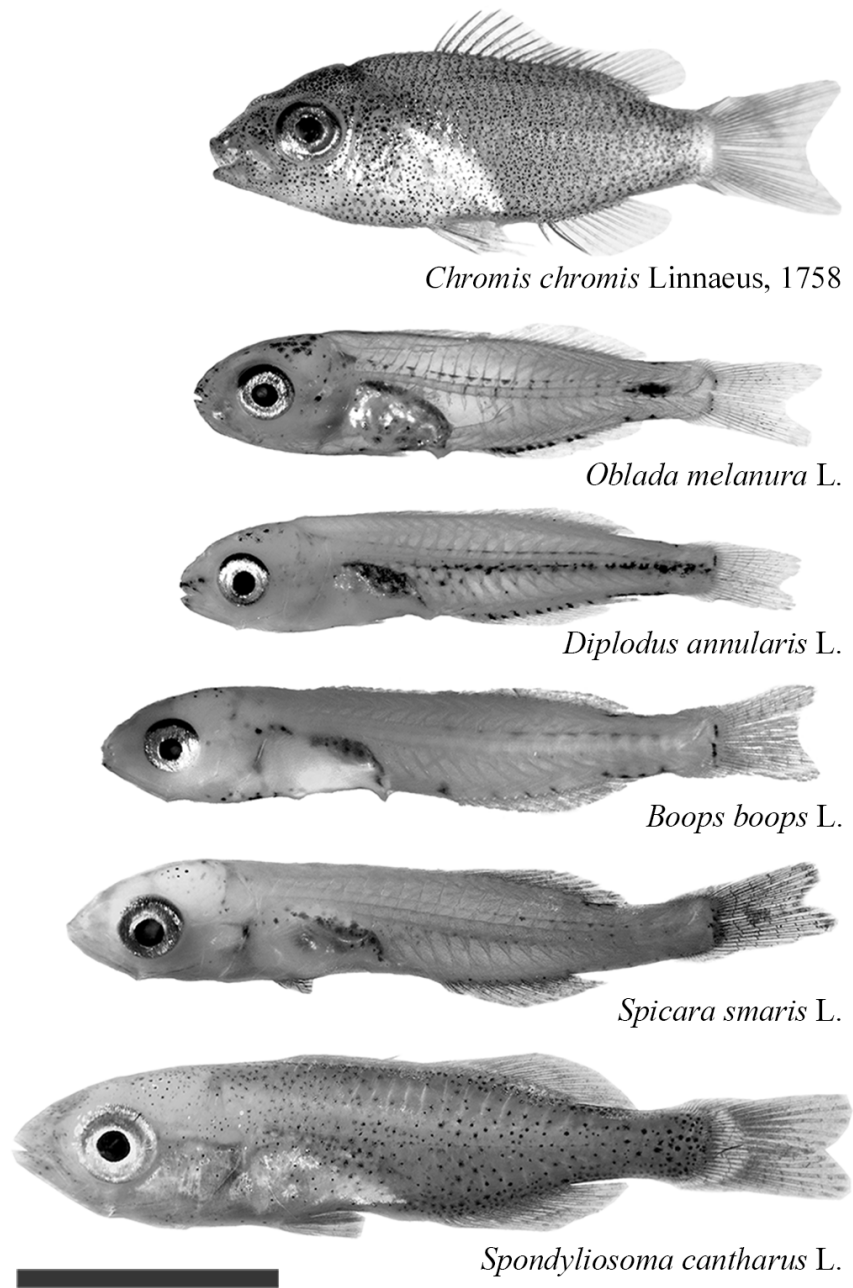


Figure 5.2: **Morphology of the settlement-stage larvae of the six species tested.** Size on the figure is proportional to median standard length (scale bar = 5 mm). Species are ordered by increasing size.

5.2.2 *DISC description and deployment*

The Drifting In Situ Chamber (DISC) is described in [122, 281]. Our configuration is presented in Figure 5.3. Briefly, it is comprised of a surface buoy that carries a GPS, an acrylic frame, a circular behavioural observation chamber (21 cm diameter x 10 cm height), a GoPro Hero 3+ camera looking upward at the chamber, a custom-made, Arduino-based, numerical compass (plus 3 backup analogical ones) to track its rotation and a cruciform Microstar Pacific Gyre drogue to lock it into the current.

The DISC is embedded in and drifts with the surrounding water mass, just like larvae would in their natural environment, allowing the larval fish to be observed with no human intervention. To reduce interaction between the structure and environmental cues (sounds, odors, light, etc.), the acrylic of the frame is transparent and has approximately the same density as seawater and the observation chamber is made of mesh (1 mm opening) on the top and the side wall. The cruciform drogue keeps the DISC locked in the current while it interacts with the turbulent flow and rotates slowly. The trajectory of the larva within the chamber informs on its orientation, which will compensate for the DISC rotation if the larva targets a fixed bearing.

Deployments were carried out from a motorboat offshore a cape (Figure 5.1). Distances to the coast ranged between 200 m and 2800 m. Depth always exceeded 100 m and was most often >300 m, which prevented visual cues from the bottom. At the start of each deployment, the DISC was pulled to the surface and a fish larva was placed in the behavioural chamber. The DISC was then lowered to the observation depth of 5 m. Each deployment lasted 20 min: 5 min of acclimation and 15 min of observation. Time, GPS position, weather conditions at start and end of DISC deployments, as well as approximate position of boats cruising within 300 m of the instrument were recorded.

5.2.3 *Data processing*

The camera produced 5 megapixel images of the fish larva in the chamber at 5 seconds intervals. The position of the larva was recorded on each image by clicking on it through a graphical user interface. Each position was converted to polar coordinates relative to the axis from the centre of the chamber to the top of the picture. The angular part of the coordinate was converted to a bearing relative to the North by subtracting the bearing of the top of the picture, recorded by the digital compass. The bearings of the position of the larva were the base data to detect cardinal orientation.

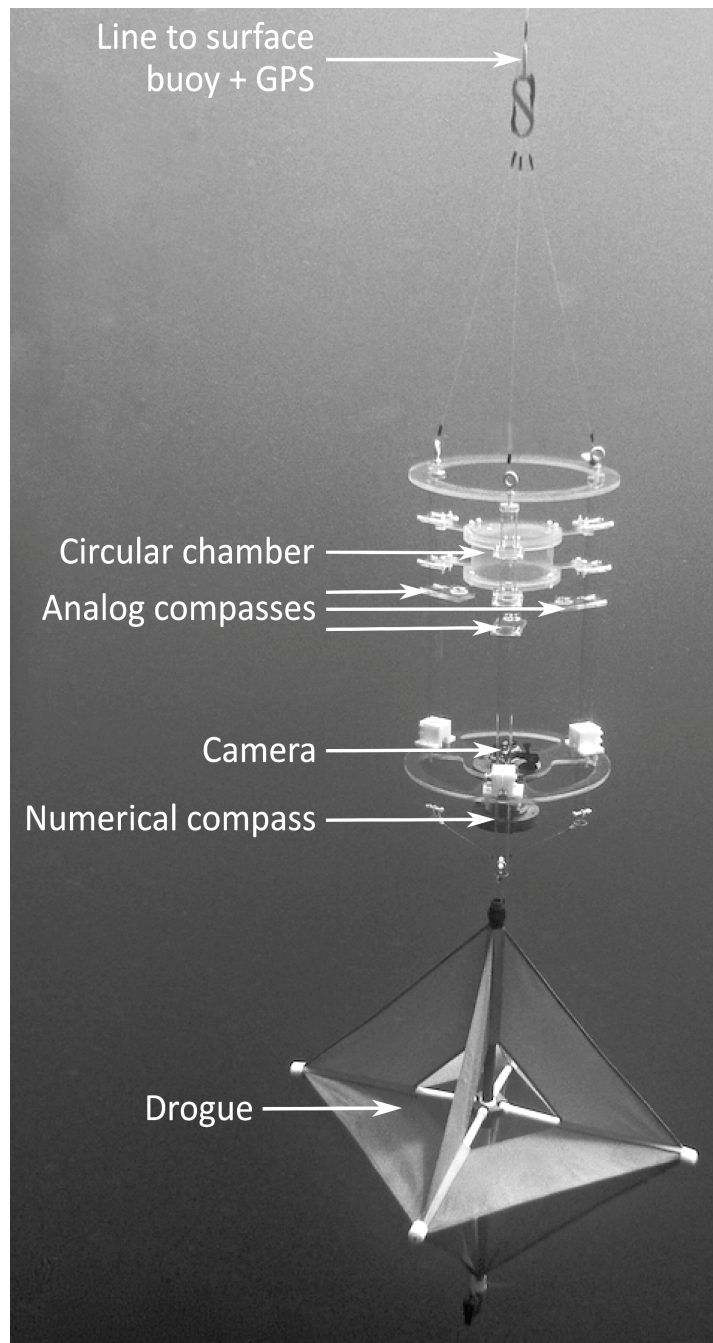


Figure 5.3: Side view of the DISC during a deployment.

In addition to cardinal orientation, the influence of various environmental cues was investigated. The direction and proximity of the coast may influence fish larvae seeking a coastal settlement habitat. In the vicinity of the deployment sites, the underwater landscape is homogeneous and consists of rocky reefs intertwined with seagrass beds. Therefore, for each deployment, the closest shore point was considered as a potential settlement habitat and the bearing and distance to it were computed from digitised coastline coordinates.

The sun was considered as a possible directional cue. Its azimuth (bearing of the solar disk) was computed from location and UTC time using [282]. A solar hour index was computed as:

$$\text{solar index} = \frac{t_{\text{deployment}} - t_{\text{sunrise}}}{t_{\text{sunset}} - t_{\text{sunrise}}}$$

where $t_{\text{deployment}}$ is the mean time of the deployment and t_{sunrise} and t_{sunset} are the sunrise and sunset times on the day of the deployment. This solar hour index ranges from 0 at sunrise to 1 at sunset; 0.5 is the time when the sun is highest in the sky. It combines the effect of the zenith (angle from the vertical) and azimuth (bearing) of the sun, which are highly interdependent.

Wind, waves and cloud cover may affect the solar signal. Meteorological data were obtained from Nice airport, located 8 km SW of the sampling zone. They included hourly averages of cloud cover (number of 1/8th of sky occupied by clouds), wind bearing and wind speed (m s^{-1}).

The drift direction and speed of the DISC were compared with larval orientation direction and strength to confirm that larvae did not simply orient into the current, which would be rheotaxis rather than orientation. Finally, the effects of other potentially confounding factors were considered, such as larva size, number of ships cruising by and presence of predators on the pictures.

5.2.4 Statistical analyses

Within-run analyses (at the individual level)

For each deployment, the ability of an individual larva to keep a bearing was tested using the Rayleigh test on the bearings of its positions in the chamber [283]. The test computes a statistic (r in $[0,1]$), which is a measure of the concentration of the positions of an individual fish larva around its mean bearing (i.e. its *directionality*) and an associated p -value.

Non-parametric procedures were used to test for differences in directionality between species, because r is bounded in $[0,1]$ and thus not normally distributed (Kruskal-Wallis test, pairwise Wilcoxon tests

with Benjamini-Hochberg correction for multiple testing and Fligner test). To test the influence of continuous environmental variables on directionality, r was logit-transformed and regressed on solar index, wind speed, current speed, distance to the coast and cloud cover using simple linear regression. The logit function is commonly used to transform values from $[0,1]$ into $]-\infty,+\infty[$ (probabilities for example). The trajectory of the sun in the sky is parabolic and its bearing is easier to assess in the morning and evening, when the sun is low in the sky. This may cause a quadratic rather than linear response to solar index, so both potential relationships were tested. The Shapiro test was used to test the normality of residuals of each significant linear model.

Across-run analyses (at the population level)

Within-run analyses only assess the ability to keep a bearing. Across-run analyses are necessary for statistical testing of *orientation* towards a common bearing, at the population level. We considered the mean bearings of directional larvae as new data and performed another Rayleigh test. The r statistic of this new test is a measure of the concentration of individual bearings around the mean direction of the population (i.e. orientation *precision*).

To test the influence of directional environmental cues on orientation (direction of the coast, the sun, the wind, the current), we computed the angle between the mean bearing of each fish larva and the bearing of the cue at the time of its deployment. As examples, the resulting angle is 0° if a larva oriented towards the cue and 180° if it oriented away from it. These bearings relative to a cue were also tested with Rayleigh tests, to determine the significance of the effect of the cue on orientation. The dispersion of the relative bearings around their mean is an estimate of the magnitude of the effect of the cue (low dispersion = large effect). This is quantified by the value of r in the Rayleigh test (large r = large effect). When the Rayleigh test was significant for several directional cues, the Wallraff test [283] was used to test for significant differences in dispersion between cues.

Remarks on the Rayleigh test

The Rayleigh test is central in this study. Its null hypothesis is randomness in the distribution of bearings. So the alternative is only a “non-random” (typically one-sided) distribution of bearings [283]. But, when the parent distribution of bearings is unimodal (or even better, a von Mises distribution), then a significant Rayleigh test proves not only non-randomness, but also concentration of bearings around the mean direction (i.e. directionality in within-run tests and orienta-

tion in across-run tests) [283]. A large sample size ($n \geq 30$) is preferable to detect unimodality and allows unimodal distributions to tend towards a von Mises distribution [283]. In within-run analyses, the sample size was 180 (one position every 5 seconds for 15 minutes). We restricted across-run Rayleigh tests to species with more than 30 directional individuals.

Data analysis tools

Circular analyses were done in R version 3.1.2 [171] with package `circular` (0.4-7). DISC data were processed with the open-source software package `discr` (<https://github.com/jiho/discr>) modified from [284]. Plots were produced with package `ggplot2` (1.0.1).

5.2.5 *Data cleanup*

To detect orientation behaviour that may be an artifact related to the DISC structure itself (e.g. larvae that oriented relative to the DISC structure, thereby not responding to environmental cues), we identified deployments where the DISC rotated at least 180° and where positions were much more concentrated in the reference of the chamber (r_{chamber}) than in a cardinal direction (r_{card}) ($r_{\text{chamber}} - r_{\text{card}} > 0.17$, a threshold based on the bimodality of the $r_{\text{chamber}} - r_{\text{card}}$ distribution). These deployments were then visually inspected to confirm the presence of the artifact. Five deployment were rejected on this basis. Three more deployments were rejected because the presence of predators around the instrument visibly affected the position of the fish larva in the chamber. The number of boats cruising in the vicinity increased directionality, although only for *O. melanura* larvae ($F=0.94$, $R_{\text{adj}}^2=0.16$, $p=0.014$). Two more deployments involving *O. melanura* were rejected because more than three vessels cruised by within the 15 min of deployment.

5.3 RESULTS

A total of 182 fish larvae were tested (sample size and body size in Table 5.1; pictures in Figure 5.2). All six species were considered for comparisons of directionality among species. Orientation analysis was restricted to *C. chromis*, *D. annularis*, *S. smarís* and *O. melanura* for which at least 30 individuals were observed.

Table 5.1: Species tested in this study: taxonomy, sample size (n) and standard length in mm (median [minimum-maximum]).

Family	Species	n	Standard length
Pomacentridae	<i>Chromis chromis</i>	48	9.7 mm [8.4-12.6]
Sparidae	<i>Diplodus annularis</i>	47	10.1 mm [8.5-11.8]
Sparidae	<i>Spicara smaris</i>	37	11.8 mm [9.3-13.9]
Sparidae	<i>Oblada melanura</i>	30	10.0 mm [7.9-12.0]
Sparidae	<i>Boops boops</i>	11	11.3 mm [9.6-12.1]
Sparidae	<i>Spondyllosoma cantharus</i>	9	12.8 mm [11.7-13.9]

5.3.1 Directionality

The vast majority of fish larvae tested were directional in a cardinal reference (within-run Rayleigh test, $p < 0.05$), with proportions of directional larvae ranging from 85.1% to 100% among species (Figure 5.4). Among Sparidae, *S. cantharus* demonstrated stronger directionality compared to other species (median $r = 0.59$; Fligner, $\chi^2 = 4.45$, $p = 0.48$; Kruskal-Wallis, $\chi^2 = 17.7$, $p = 0.003$; pairwise-Wilcoxon, all $p < 0.05$). Directionality was similar in the four other species of this family (*O. melanura* $r = 0.30$, *D. annularis* $r = 0.31$, *S. smaris* $r = 0.33$, *B. boops* $r = 0.40$; pairwise-Wilcoxon, all $p > 0.05$). *Chromis chromis* was significantly more directional than *O. melanura* and *D. annularis* (pairwise-Wilcoxon, all $p < 0.05$) but not significantly different from the other species.

Sun-related variables (solar index and cloud cover) influenced the directionality of larvae more than any other variable. Directionality decreased throughout the day for both *C. chromis* ($F = 1.02$, $R_{adj}^2 = 0.14$, $p = 0.007$) and *S. smaris* ($F = 0.94$, $R_{adj}^2 = 0.10$, $p = 0.034$; Figure 5.5), although the signal was very noisy. The quadratic effects of the solar index were never significant, so the decrease was considered linear. *Chromis chromis* were also much less directional under cloudier skies ($F = 0.95$, $R_{adj}^2 = 0.25$, $p < 0.001$).

In *C. chromis*, directionality appeared stronger when closer to the shore ($F = 1.03$, $R_{adj}^2 = 0.11$, $p = 0.014$). However, this result could be an indirect effect of the sun, because deployments further away from shore were often done later in the day, when r was lower. The relative effects of distance to coast and solar index were discriminated in a linear model of directionality regressed using both variables. Solar index was significant ($p = 0.035$) but distance to coast was not ($p = 0.084$), making solar hour the dominant factor and the effect of distance an artifact, caused by its unfortunate correlation with solar hour.

Furthermore, in *D. annularis* only, small larvae were more directional than larger ones ($F = 1.06$, $R_{adj}^2 = 0.12$, $p = 0.014$). Current or wind

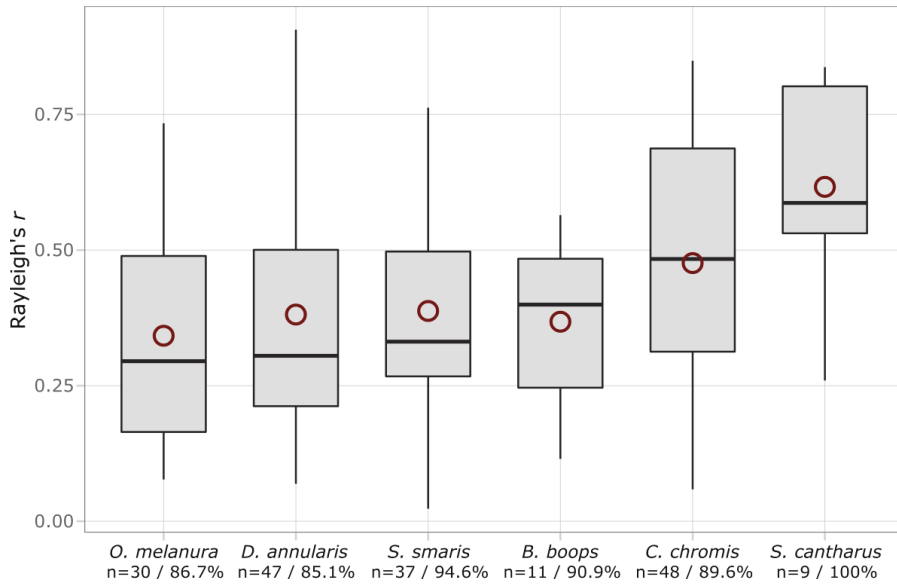


Figure 5.4: **Strength of directionality (Rayleigh's r) of the six species tested.** Sample size (n) and proportion of directional larvae (%) are indicated along the x-axis. Standard boxplots (median, interquartile range and total range) are supplemented with black dots representing mean r values.

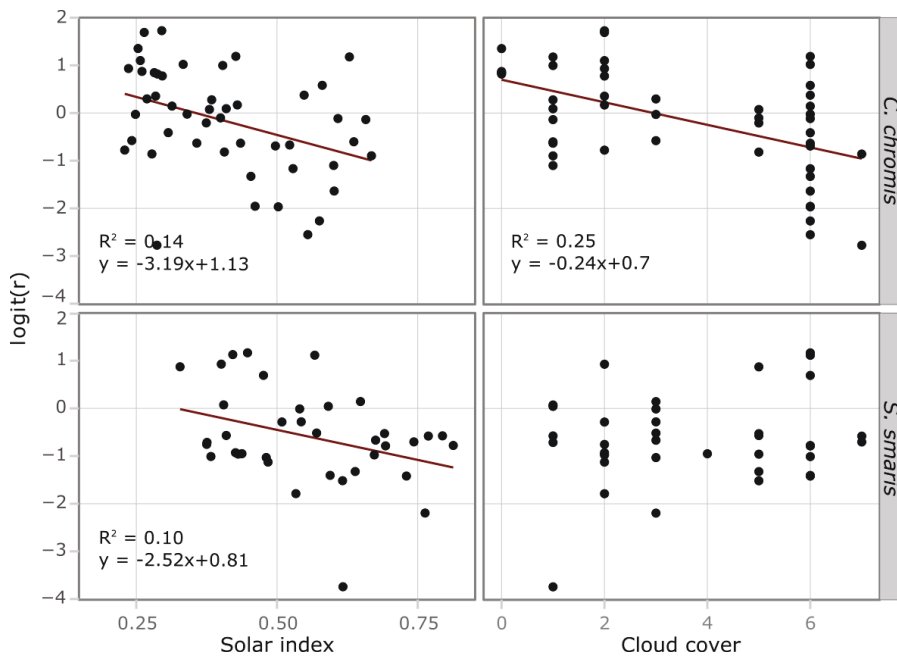


Figure 5.5: **Regressions of directionality (Rayleigh's r) on solar index and cloud cover for *C. chromis* and *S. smaris*.** Regression lines are drawn for significant relationships only. Directionality was strong in the morning and decreased linearly along the day. Directionality decreased linearly with cloud cover for *C. chromis*.

Table 5.2: Orientation relative to various cues in the four species tested.

For each species: mean angle ($^{\circ}$) relative to the cue direction (0° =towards the cue, 180° =away from it); precision of the orientation towards that angle, quantified by the across-run Rayleigh's r , ranging from 0 (no orientation) to 1 (maximum precision); p -value of the across-run Rayleigh test (p -values<0.05 are in bold).

	<i>Chromis chromis</i>			<i>Spicara smaris</i>		
	Bearing	r	p	Bearing	r	p
North	123 $^{\circ}$	0.21	0.18	188 $^{\circ}$	0.51	<0.001
Sun	204 $^{\circ}$	0.26	0.049	7 $^{\circ}$	0.52	<0.0001
Coast	13 $^{\circ}$	0.11	0.62	192 $^{\circ}$	0.50	<0.001
Wind	47 $^{\circ}$	0.17	0.28	249 $^{\circ}$	0.42	0.002
Current	324 $^{\circ}$	0.20	0.20	134 $^{\circ}$	0.32	0.028

	<i>Diplodus annularis</i>			<i>Oblada melanura</i>		
	Bearing	r	p	Bearing	r	p
North	123 $^{\circ}$	0.21	0.18	123 $^{\circ}$	0.21	0.18
Sun	329 $^{\circ}$	0.33	0.012	52 $^{\circ}$	0.17	0.49
Coast	137 $^{\circ}$	0.19	0.23	339 $^{\circ}$	0.20	0.36
Wind	211 $^{\circ}$	0.19	0.23	357 $^{\circ}$	0.11	0.76
Current	54 $^{\circ}$	0.11	0.60	48 $^{\circ}$	0.28	0.13

speeds never significantly affected directionality, in all species or the pooled assemblage.

5.3.2 Orientation

Only *S. smaris* oriented cardinally, to the south (mean bearing=188 $^{\circ}$, $r=0.51$, $p<0.001$, Figure 5.6). For the three other species, the distribution of per-deployment mean bearings was not significantly different from a uniform distribution. Yet, three species significantly oriented relative to the sun direction: *S. smaris* ($r=0.52$, $p<10^{-4}$), *D. annularis* ($r=0.33$, $p=0.012$) and *C. chromis* ($r=0.26$, $p=0.049$). They displayed contrasting orientation patterns: the Pomacentridae *C. chromis* oriented away from the sun (mean angle=207 $^{\circ}$) while the two Sparidae oriented towards it (*S. smaris*: 7 $^{\circ}$, *D. annularis*: 329 $^{\circ}$, Figure 5.6). The dispersion of angles relative to the sun was not significantly different among the three species (Wallraff, all $p>0.05$).

Oblada melanura exhibited a uniform orientation pattern relative to all tested cues. *Chromis chromis* and *D. annularis* did not significantly orient relative to any tested cue other than the sun direction. In contrast, *S. smaris* oriented significantly relative to all tested cues

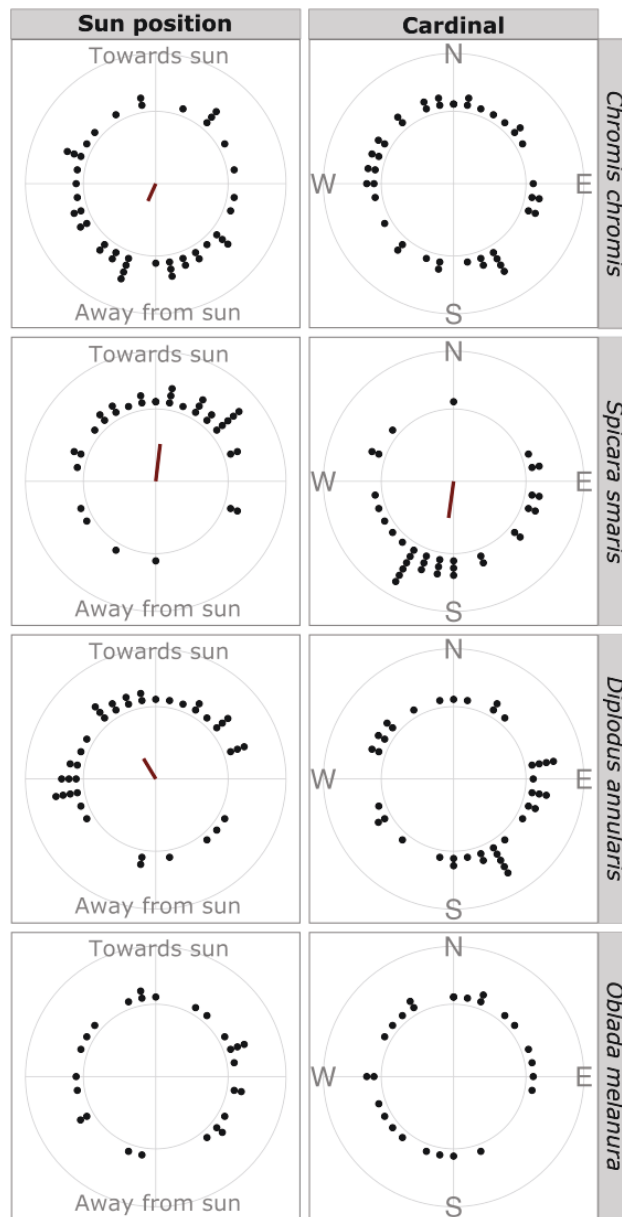


Figure 5.6: **Orientation in cardinal reference and relative to the sun direction.** Each dot represents one observation run of 15 min. Mean bearings per-run are binned over 10 degrees for plotting. The radius in the middle shows the mean direction of orientation and its length is proportional to the orientation precision (across-run Rayleigh's r).

(Table 5.2). These directional cues were partly correlated (Figure 5.7): the coast was mostly to the north, the sun was mostly to the south, wind was mostly from the east or south and current was either from the east or from the west. Still, the orientation relative to the sun direction has the highest r value ($r=0.52$, Table 5.2), while the sun itself was moving across a quite wide range (162° ; Figure 5.7). However, the angular dispersions were not significantly different between cues (Wallraff, all $p>0.05$) and we cannot be definitive regarding the relative effects of the various cues tested on the orientation in *S. smarís*.

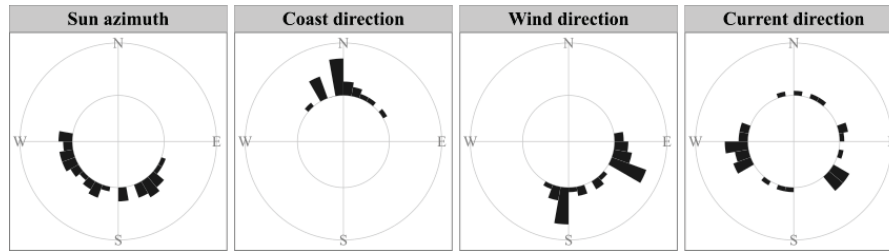


Figure 5.7: Roses of the bearings of the four environmental cues observed during 39 deployments with *S. smarís*.

5.4 DISCUSSION

5.4.1 Orientation abilities of fish larvae

These first *in-situ* observations of the orientation behaviour of wild-caught Mediterranean fish larvae showed that 89.6% kept a bearing, with a mean individual directionality of $r=0.40$. This proportion is comparable to what has been observed for the more widely studied tropical fish larvae [e.g. 116, 122, 273]. Three out of four tested species oriented relative to at least one environmental cue.

For Sparidae specifically, the proportion of directional larvae was higher for all species in our study compared to the two other studies on larvae of this family [279, 280], even though they used a different observation technique which usually yields higher directionality than the DISC [116]. This suggests that Mediterranean Sparidae are at least as capable as their southern-hemisphere counterparts.

Most orientation work has focused on Pomacentridae, using choice chambers [278], underwater following (Leis *et al.* studies summarised in [116]) and DISC [122, 274]. *C. chromis* may be compared with a congeneric species, *Chromis atripectoralis* Welander & Schultz, 1951, which has been extensively studied around Lizard Island, Australia [116]. With the same observation method (the DISC), a similar proportion of larvae were directional (about 90%) but *C. atripectoralis* was always

more directional (within-run $r=0.67$) than *C. chromis* ($r=0.48$). However, the two species may not use the same cues for orientation, as *C. atripectoralis* showed consistent orientation towards the south-west for almost all combinations of study methods, locations around the island and seasons, while *C. chromis* only oriented relative to the position of the sun in this study.

Among Mediterranean species, *O. melanura*, *D. annularis*, *S. smaris* and *B. boops* had equivalent bearing-keeping abilities at the individual level, while *S. cantharus* and *C. chromis* were both better and not significantly different from each other. Settlement-stage larvae of the first four species are similar morphologically, with small and transparent bodies of almost identical standard length (Figure 5.2, Table 5.1) and have pelagic larval durations of 16-18 days [232]. Larvae of *S. cantharus* and *C. chromis* are more muscular, thicker and more pigmented (Figure 5.2). *S. cantharus* has a longer pelagic larval duration (38 days [232]). *C. chromis* has a pelagic larval duration of about 18 days [232] but larvae hatch from benthic eggs, while others, except *S. smaris*, hatch from pelagic eggs, which are usually smaller and contain less reserves, resulting in less developed larvae at hatch. The noticeable morphological differences at settlement-stage may reflect ontogenetic differences and the better bearing-keeping abilities of *S. cantharus* and *C. chromis* may reflect a more complete development of their sensory organs. Whatever the mechanism, these results highlighted that orientation ability is likely not general to taxonomic groups, but may be related to morphology and ontogenetic development. Therefore, extrapolation to non-observed species, as is common in modeling purposes, should be made with caution. Gathering more empirical data on larval fish behaviour is necessary to make informed parameterisation of models or general inferences on community connectivity.

5.4.2 Sun-based orientation in the open ocean

Among the environmental cues tested, sun-related variables such as sun azimuth, solar index and cloud cover were the variables that most often influenced directionality and orientation in this study. The use of celestial cues by fish larvae for orientation has been demonstrated in one tropical species and location, through a laboratory experiment [124]. It has also been suggested *in situ* by the significant effects of time of day [116, 273] and cloud cover [116, 273, 274] on directionality and orientation precision, because time of day and cloud cover affect downwelling light signals and direct view of the sun. With no evidence so far for magnetic orientation in fish larvae, celestial orientation is the only mechanism that could enable large-scale navigation.

Indeed, while fish larvae respond to coastal sounds [117], they cannot detect such ambient sounds more than a few hundred metres away from their source [118]. Odors may travel far from their source but, at the scale of centimetre-long larvae, their diffusion is turbulent and extracting directional information from it would be complex [122].

Here, *C. chromis* was less directional under cloudy skies; a result that others have interpreted as indicative of a sun compass [274]. Directionality (within-run r) decreased linearly during the day for *C. chromis* and *S. smarís*, which also suggests the use of the sun as a bearing-keeping cue [116]. In fact, those two variables (cloud cover and solar hour) were the only ones influencing directionality in *S. smarís* and *C. chromis*. A quadratic relationship would have been expected between r and solar hour, whereby r is high at the beginning and end of the day, when the sun is low in the sky and provides a good directional reference and low around midday, when the azimuth of the sun is more difficult to assess. The linearity of the decrease observed here, more specifically the lack of increase in the afternoon, may be due to increasing nebulosity along the day and to mountains west of the observation location, both of which mask the sun in the evening.

Orientation of *C. chromis* and *D. annularis* was significant only relative to the sun azimuth, not relative to any of the four other cues tested, providing direct *in situ* evidence of sun-based orientation. For *S. smarís*, orientation was significant relative to all tested cues, but the bearings of the cues were correlated and no one cue could be distinguished as significantly more influential than the others. Still, sun-based orientation seems likely for *S. smarís* also, because its directionality was correlated to the solar index and its orientation precision (across-run r) was higher relative to the sun azimuth than to other cues.

Orientation relative to the coast was only significant for *S. smarís* and distance to the coast affected directionality in *C. chromis* only, but was an artifact of the sampling design. So, in the oceanic environment in which larvae were tested (bottom depth >300 m and distance from coast often >500 m), it seems they did not react to or could not detect coast-related cues. Without such a point of reference, we hypothesise that larvae used sun-related cues to orient in a fixed direction. The late stages of these species are active swimmers and can travel several kilometres in a few hours [Chapter 6]. They could therefore rapidly reach the vicinity of the coast if they swam towards it and get within the detection range of coast-based cues. The combination of large scale and small scale orientation with efficient swimming can drastically affect larval dispersal trajectories and help locate favourable settlement habitats [89].

This study was conducted in summer, around 44°N , where the sun at its zenith is about 20° from the vertical and thus always to the south. Interestingly, the two families tested presented contrasting orientation patterns: Pomacentridae oriented away from the sun, Sparidae oriented towards the sun. Comparing the direction of orientation relative to the sun and the direction of drift in the DISC did not highlight any drift-compensation pattern (e.g. orientation bias towards the east of the sun when the DISC drifted towards the west). Both observations suggest that the sun may have been used as a reference, a compass for orientation, rather than as an actual goal for navigation. Navigation is the process of ascertaining the position of a goal and following a route to reach it; it is different from (and more complex than) orientation, which is the action of moving based on a compass, not a route. Based on our data, it is difficult to draw a conclusion regarding navigation as larvae were in a space-limited environment and tracked for only 15 minutes. However, the orientation patterns that we observed may be interpreted as larvae calibrating a compass against a universally available cue: the sun's azimuth. This mechanism was proved possible in settlement-stage fish larvae by a clock-shifting experiment [124]. Furthermore, the sun itself would make little sense as a goal for navigation; its position constantly changes and is not always indicative of the position of a settlement habitat, a food source or other goals relevant for the survival of fish larvae.

Multiple physiological mechanisms could mediate such a sun-based compass, including direct vision of the sun and detection of skylight polarisation. Some Pomacentridae can discriminate light polarisation and use it for orientation in certain conditions (adults [285]; settlement-stage larvae [274]). For larvae, the vast majority of individuals tested favoured direct vision of sun position over polarisation axis [274]. Yet, direct vision of the sun from underwater is hampered by clouds or rough seas. In contrast, polarisation patterns are equivalent under clear or cloudy skies [286]. Wind speed and sea state never influenced results and cloud cover affected directionality in *C. chromis* but not in the three Sparidae. So both direct vision and detection of light polarisation might have been used by the species observed here to detect the direction of the sun. Determining which mechanism is primarily used for orientation is impossible without additional experiments and direct cue manipulations. Improved understanding of the differences in the utilisation of sun-related signals between the two families may explain their opposing orientation relative to sun position.

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SWIMMING SPEEDS OF MEDITERRANEAN SETTLEMENT-STAGE FISH LARVAE NUANCE HJORT'S ABERRANT DRIFT HYPOTHESIS

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6.1 INTRODUCTION

Over a century ago, in a founding publication, Hjort suggested that survival of early life stages determine adult fish populations [1]. As presented in the introduction (Section 1.2, p. 27), he postulated two main hypotheses: first, larval fish pools may be depleted by starvation if prey are not available during the “critical period” of first-feeding; second, larvae are transported by currents and face important mortality if they “aberrant[ly] drift” away from favorable recruitment sites. Built on observations on a few cold-temperate species, those hypotheses have generalised and form the basis for the understanding of the larval phase of fish in all oceans. Most attention has been focused on the critical period, leading to other feeding-related mechanisms such as the “match-mismatch” [287], the “stable ocean” [288], and the “optimal environmental window” hypotheses [22]. All three identify environmental conditions favorable for first-feeding by fish larvae that should therefore result in higher recruitment, as explained in the introduction (Section 1.2, p. 27). Fewer studies dealt with the *aberrant drift* hypothesis [15], except for the “larval retention/membership-vagrancy” hypothesis [26, 27]. This *member/vagrant* hypothesis states that physical retention of early-life stages is critical for recruitment and is dependent on adult spawning in appropriate places, when and where conditions are conducive for eggs and larvae retention.

While dispersal can range up to hundreds of kilometres in some marine organisms [70], high self-recruitment rates have been observed in others [84, 87, 121]. The levels of self-recruitment measured in species with a pelagic larval phase are unlikely to occur with passively

drifting particles [83]; physical retention cannot be the only explanatory mechanism. In the meantime, fish larvae have been shown to have non-negligible swimming abilities and, at least in some Perciformes species, to be able to swim in an oriented manner in the open ocean (reviewed in [228] and shown in Chapter 5 for our species of interest). Fish larvae may therefore have the potential to influence their dispersal [273, 289–291], but the actual quantitative consequences of this potential remain largely unexplored.

Various methods are used to study larval fish dispersal [75] although modeling is the only approach that enables consideration of the effect of larval behaviour throughout the pelagic larval phase [269, 292]. In most modeling studies, the outcomes of simulations including larval swimming behaviour resulted in striking differences compared to simulations with passively drifting larvae. For example, vertical swimming was necessary to match observed ichthyoplankton distributions around Barbados [93]; downward vertical swimming of 1 to 3 cm s⁻¹ greatly enhanced larval retention on the shelf in Georges Bank, Newfoundland and Norway [293–295]; horizontal swimming towards the shore during the larval phase resulted in a marked improvement in recruitment rate in Florida or the Great Barrier Reef [89, 296, 297]; early horizontal swimming and increasing behavioural abilities along larval development reduced dispersal distance and improved settlement along the Florida Keys [275].

Different ways to measure swimming abilities appear in the literature and target different ecological questions (reviewed in [100]). The most relevant for dispersal models are endurance, *in situ* speed and critical speed.

Endurance is measured by making larvae swim against a flow at a fixed speed (usually 13.5 cm s⁻¹) until they cannot sustain this speed anymore. This is an estimation of the distance that fish larvae could potentially swim in a typical coastal environment. For instance, settlement-stage larvae of 24 species of Pomacentridae were able to travel an average of 25 km without feeding or resting [114]. Feeding larvae during trials at least doubled, often tripled, their endurance [298].

In situ swimming speed is measured by scuba divers following a larva that moves in its natural environment. In 60 tropical species, *in situ* speed was often around 15–20 cm s⁻¹ [100]. This speed is assumed to be the best available measure of what larvae actually do in the field and should be sustainable over a very long time, because larvae are not forced to swim and feed while swimming [100].

Critical swimming speed (U_{crit}) is measured by swimming larvae against a flow of known speed, increasing the speed at regular intervals until the larva fatigues. As such, it quantifies a combination

of forced swimming speed and endurance, in a standardised manner [299]. Because it is standardised, it has been used to compare tropical and temperate species. Cold temperatures slow growth down [300], so settlement-stage of temperate fish larvae were expected to be poorer swimmers than their tropical counterparts. Nevertheless, in Perciformes, the difference might actually be limited, as some temperate species swam at up to 30 cm s^{-1} [291, 301]. Still, such comparisons are scarce because U_{crit} has only been measured in 20 temperate Perciformes species, including both reared [100, 301–305] and wild-caught larvae [113, 291], while U_{crit} has been published for >100 Perciformes coral reef fish species [114, 306–311]. In the tropics, U_{crit} ranges from 5 to $>60 \text{ cm s}^{-1}$ with a mode around 30 cm s^{-1} . Noticeably, U_{crit} was equal to twice the *in situ* speed in most Perciformes species in which the comparison was possible [308], so U_{crit} can be used to estimate the more biologically-meaningful *in situ* speed.

In this study, we measured the critical swimming speed of settlement-stage larvae of coastal temperate fish species, for which no data were available. We focused on competent fish larvae, at the end of their pelagic larval phase, which are well developed, may swim fast and need to rapidly find a suitable habitat to settle [100]. Then, we included those observed values of swimming speed in a Lagrangian dispersal model forced by realistic current fields to determine how far offshore a larva could drift and still be able to swim back to the coast within its competency period.

6.2 MATERIALS AND METHODS

6.2.1 Study area

The Ligurian Sea and Liguro-Provençal current has been extensively described in the previous chapters. We stress again that: (i) the continental shelf is very narrow and the offshore expansion of adult populations of coastal fish species is thus very limited; (ii) the Liguro-Provençal current (Figure 6.1) is believed to act as a potential barrier to offshore export of coastal particles [146–148, 312].

Fish settlement-stage larvae (hereafter referred as *fish larvae*) used in the experiments were caught in the Bay of Villefranche-sur-Mer (43.69°N , 7.31°E). As explained in Chapter 4, the bay is open to oceanic waters (bottom depth drops to $>300 \text{ m}$ at the mouth of the bay; Figure 6.1) and is known to host rich oceanic plankton communities [192]. The bay may also be a nursery area, thanks to its numerous seagrass beds [237].

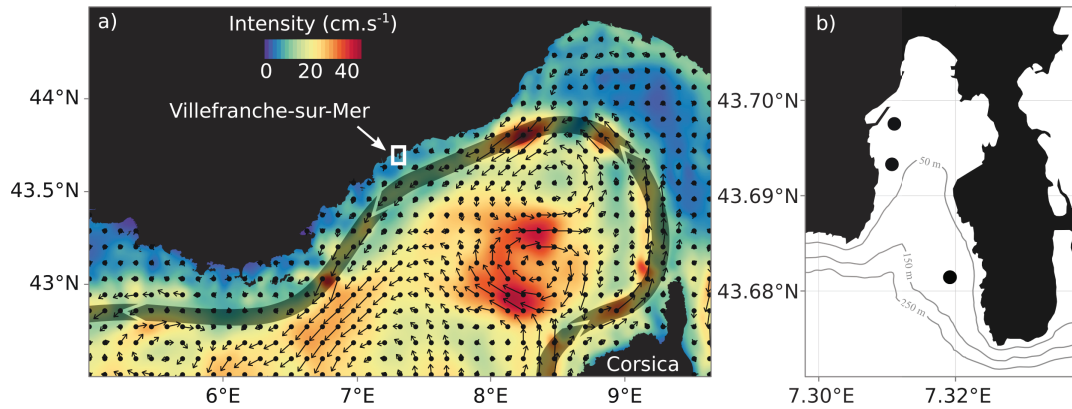


Figure 6.1: **a) Simulated current field at 5 m depth, averaged over June 2014** (source: MARS₃DMed, PREVIMER). The color scale depicts average current velocity. The arrows are average current vectors (showing both velocity and direction). The dots at their origin represent the 550 release sites in the modeling experiment (see Section 6.2.3, p. 146). The shaded line indicates the average position of the Ligurian current; but the current meanders, particularly along the northern coast, hence the weak signal in terms of *average* velocity. It creates two stable eddies with high average current velocities between Corsica and the continent: a strong anticyclone in the center and a weaker cyclone in the north. **b) Collection sites of fish larvae (dots) in the Bay of Villefranche-sur-Mer, France**, which location is indicated by the white rectangle on panel a).

Table 6.1: **List of tested species.** Taxonomy, number of individuals tested (n) and standard length (SL) in mm: mean \pm standard deviation (SD) and [range].

Family			
Species	n	SL \pm SD	[min-max]
Mugilidae			
Mugilidae sp.	10	12.2 \pm 1.1	[9.8-13.4]
Pomacentridae			
<i>Chromis chromis</i> Linnaeus, 1758	33	9.9 \pm 1.1	[8.3-12.4]
Sparidae			
<i>Boops boops</i> L.	40	10.9 \pm 1.2	[8.2-13.8]
<i>Diplodus annularis</i> L.	26	9.0 \pm 1.0	[7.8-11.6]
<i>Spicara smaris</i> L.	31	11.8 \pm 1.2	[9.0-13.9]
<i>SpondylIOSoma cantharus</i> L.	9	13.4 \pm 1.7	[11.7-17.3]
<i>Dentex dentex</i> L.	1	15<SL<20 ¹	
<i>Oblada melanura</i> L.	1	9.6	
<i>Pagellus acarne</i> Risso, 1827	1	20.6	
<i>Pagrus pagrus</i> L.	1	14.9	

¹The standard length of *Dentex dentex* is reported as an approximate range only because the specimen was kept alive after the experiment and its exact size could not be measured with certainty.

6.2.2 Swimming speed

Fish larvae collection

This study was concurrent with that of Chapter 5 and the collection of fish larvae was the same: three CARE light-traps deployed four nights a week between May and July 2014 (for more details see Chapter 4). After collection, fish larvae were sorted visually and kept in 30 L buckets. In the laboratory, buckets were placed in a temperature-controlled room at 19°C (close to or slightly lower than seawater temperature measured *in situ*). Every effort was made to minimise stress to the specimens: larvae were sorted with small water containers (never hand-nets), were never exposed to intense light sources and the room was kept as quiet as possible.

We focused on six common and abundant species. In four others, only one individual was tested but its speed was reported for completeness and because absolutely no data exists on those species (Table 6.1).

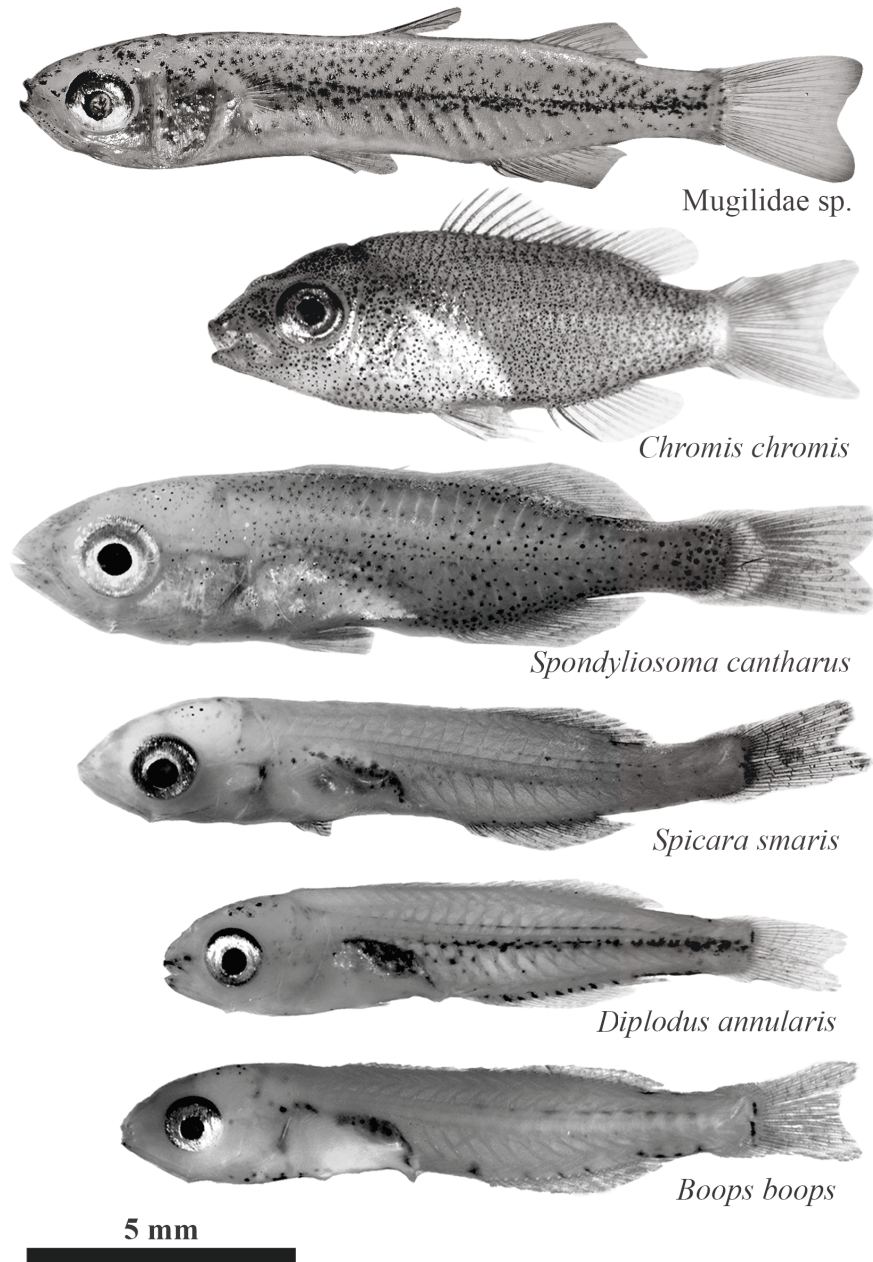


Figure 6.2: Morphology of the six species tested. Species are sorted in decreasing order of swimming speed, from top to bottom.

Measurement of critical speed

Swimming speeds were measured with a Loligo Systems swimming chamber (model #SW10000). It comprises a 30 L ambient tank, a cylindrical swimming tunnel of 26.4 mm diameter x 100 mm length (170 mL) and a speed controller. The flow speed inside the tunnel was calibrated by filming fluorescent micro spheres of neutral density at 120 frames per second and estimating the time spent to travel a fixed distance by counting the number of frames. Flow speed was measured 10 times for 12 positions of the speed controller. This allowed us to verify that flow speed varied completely linearly with speed controller values, as per the manufacturer's specification ($y = 7.4x - 2.9$, $F=4333$, $R^2=0.97$, $p<10^{-16}$). This linear relationship was used to compute flow speed from controller graduation.

Critical swimming speed (U_{crit}) was measured by increasing flow speed by 1.9 cm s^{-1} every 5 min until the larva fatigued and could not hold its position in the tunnel. This protocol avoids overestimating U_{crit} , as shorter time-steps would give more importance to maximum swimming speed than endurance [298]. U_{crit} was computed using the formula provided by [313]:

$$U_{crit} = U + \frac{t}{t_i U_i}$$

where U is the penultimate speed (the last one for which the larva swam the full 5 min), U_i the speed increment (1.9 cm s^{-1}), t the time swum at the final speed (in s) and t_i the time increment (5 min = 300 s).

A total of 153 larvae were tested; 77% on the day of their capture, 91% within 24h and all within 3 days. After observation, fish larvae were identified to species-level based on [154, 156, 157]. Their standard length was measured to the closest 0.1 mm using an image capture software under a stereomicroscope (Nikon NIS Element 4.11 D).

Data analysis

To determine if the hydrological environment in which larvae swam was inertial or viscous, we computed the Reynolds number (Re) as:

$$Re = U_{crit} L_{SL} / \nu$$

where U_{crit} is the measured critical swimming speed, L_{SL} the standard length and ν the kinematic viscosity of sea water ($1.03 \cdot 10^{-6} \text{ m}^2 \text{ s}^{-1}$ at 20°C) [314].

The influence of the delay between larvae collection and speed measurement on U_{crit} was checked per species with a Kruskal-Wallis test using the number of days since collection as the grouping variable. U_{crit} was also compared among species, sites and collection

dates using non-parametric procedures, because residuals of parametric analyses were never normally distributed. Kruskal-Wallis and pairwise Wilcoxon tests with Benjamini-Hochberg correction for multiple testing [315] were used to compare medians and Fligner test to compare variances [316]. To test the usual assumption that swimming speed increases with size [16], U_{crit} was regressed on standard length; linear, exponential and logarithmic relationships were assessed and the Shapiro test was applied on residuals to check their normality.

6.2.3 Modeling experiment

Hydrodynamic and lagrangian models

Ocean current fields were provided by MARS3DMed (IFREMER). This model is described in details in [317] and has been validated with observations [318]. Current fields are available every 3 hours, with a $1/64^\circ$ grid size (ca. 1.2 km in this region), over 60 sigma layers. The modeled domain covers most of the NW Mediterranean Sea, from 0°E to 15°E and 39.5°N to 44.5°N . We used current fields of June 2014, i.e. when larval fish settlement was at its peak in 2014 [Chapter 4] and when most critical speeds were measured in this study.

Virtual larvae were simulated using the Connectivity Modeling System (CMS) [319]. This open-source Lagrangian model is particularly adapted to assess the influence of directional swimming because it comprises a biased and correlated random walk submodel that allows controlling the swimming speed and cone of orientation of particles, as described in [275]. In this Lagrangian model, horizontal diffusivity was set to $5.5 \text{ cm}^2 \text{ s}^{-1}$ based on diffusions diagrams from [320]. The time-step was set to 1800 seconds, $1/6^{\text{th}}$ of the hydrodynamic model output time-step.

Simulations scenarios

The goal of this simulation exercise was to offer a contrasting view compared to most models that simulate passive or only vertically-migrating larvae [269, 321]. Mortality, vertical migration, feeding and growth were not considered and focus was put on horizontal swimming. We simulated late-stage larvae that constantly swam, always oriented towards the coast with good precision ($k=4$ in the CMS, see [276] for sensitivity analysis of the k parametre) and could successfully settle as soon as they reached the coastal area (1.5 grid points from the shore, ca. 2 km away from it). While this can seem caricatured, fish larvae are capable of swimming directionally in the ocean, over short distances using coastal cues [100] and also over long distance using celestial cues [Chapter 5]. We only simulated the compet-

ency period, which is four days on average for the species studied [232]. At this point in their larval life, sensory and locomotive organs are well developed (Figure 6.2, [16]); larvae can swim and feed efficiently. Finally, swimming speed was set to half of the measured critical speeds, which is a good estimate of their *in situ* speed [308], a speed at which other species have been observed to feed on the go [253]. In addition, Leis & Clark [298] observed that, while unfed larvae of several species of Pomacentridae swam “only” 21 km, they reached 63 km on average when fed once per day throughout the swimming experiment and some even kept growing. It showcases that fish larvae may have high swimming endurance in their natural environment and should be able to sustain swimming at reasonable speeds over extended periods of time.

More precisely, 7 simulations were run: one passive and six with horizontal swimming speed set based on measured U_{crit} (see Section 6.3.1, p. 148 and Table 6.2 for values). To capture temporal and spatial variability, for each simulation, 50 virtual larvae were released at three depths (1, 5 and 15 m), at midnight every day, for 25 days, at sites distributed on a 8 km grid over the Ligurian Sea. This configuration was based on the assumption that, at the start of the simulation, late-stage larvae could be anywhere in a domain ranging from 42.5°N to 44.5°N and from 5°E to 10°E (550 sites in total; Figure 6.1). That amounted to over two millions ($n=2,062,500$) larvae tracked per simulation.

Data analysis

For each simulation, the proportion of successful settlers among the two millions simulated larvae was computed as the number of virtual larvae that entered the coastal area within four days. The proportion of settlers was then regressed against swimming speed to quantify the increase in settlement associated with increased swimming abilities. The origin of successful settlers were mapped by computing the probability of settlement from each release site, integrated over the three depths and linearly interpolating it over the simulation domain. To quantify how swimming speed influenced the distance from the coast up to which a significant proportion of larvae could still settle, the distance between the coast and the 0.5 settlement probability isoline was computed and averaged over the domain.

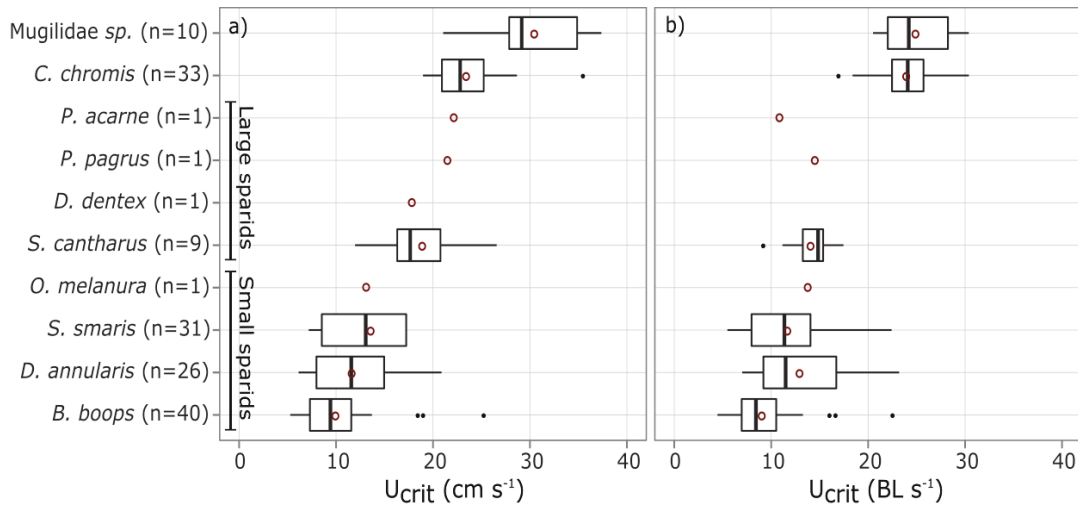


Figure 6.3: Critical swimming speed in a) cm s^{-1} and b) in body length per second (BL s^{-1}). The mean values (empty circle) are overlaid over standard boxplots. Two groups of Sparidae species were highlighted: large, fast species and smaller, slenderer, slower species; differences in swimming speed were significant between groups but often not within group. With speeds in BL s^{-1} , all Sparidae were similar.

6.3 RESULTS

6.3.1 Swimming speed

Swimming speed was not significantly different among collection sites or collection dates (Kruskal-Wallis, $p > 0.05$ for all species). The delay between collection and experiment did not influence swimming speed either (Kruskal-Wallis, $p > 0.05$ for all species), so all data were pooled in the following.

Critical swimming speeds ranged from 5.3 to 37.4 cm s^{-1} (Figure 6.3, Table 6.2). Among statistically comparable species, pairwise tests highlighted that Mugilidae sp. were significantly faster than all others, followed by *C. chromis* and then *S. cantharus*, while *S. smarís*, *D. annularis* and *B. boops* were similar to each other.

In four species, a single individual was tested. *Dentex dentex*, *P. pagrus* and *P. acarne* presented U_{crit} comparable with *S. cantharus* (Table 6.2, Figure 6.3) and were associated in a “large sparids” group, because settlement-stage larvae of these four species are large (mean SL = 14.2 mm), muscular, pigmented and have well developed fins. *Oblada melanura* swam at 13.1 cm s^{-1} , which is very close to U_{crit} of *B. boops*, *D. annularis* and *S. smarís* (Table 6.2, Figure 6.3). These four species were thus grouped together as “small sparids”, because their post-larvae are all smaller (mean SL = 9.7 mm), slenderer, less pig-

Table 6.2: **Sample size (n), critical swimming speed (U_{crit}) in cm s^{-1} and BL s^{-1} and estimated *in situ* speed.** Results are presented per species, for the two morphological groups of sparids and for the slowest and fastest individuals overall. *In situ* speeds used in the model were estimated as about half of U_{crit} [100].

Family		U_{crit} (cm s^{-1})	U_{crit} (BL s^{-1})	Estimated
Species	n	med \pm mad [min-max]	med \pm mad [min-max]	<i>in situ</i> speed
Mugilidae				
Mugilidae sp.	10	29.2 \pm 5.1 [21.1-37.4]	24.2 \pm 3.7 [20.5-30.4]	15 cm s^{-1}
Pomacentridae				
<i>C. chromis</i>	33	22.8 \pm 3.0 [19.0-35.6]	24.1 \pm 2.4 [17.0-30.4]	12 cm s^{-1}
Sparidae				
Large sparids	12	19.2 \pm 3.8 [12.0-26.6]	14.40 \pm 1.7 [9.3-17.5]	10 cm s^{-1}
<i>P. acarne</i>	1	22.1	10.7	
<i>P. pagrus</i>	1	21.5	14.4	
<i>D. dentex</i>	1	17.8	$9 < U_{crit} < 12$	
<i>S. cantharus</i>	9	17.7 \pm 4.4 [12.0-26.6]	14.8 \pm 2.3 [9.3-17.5]	
Small sparids	98	11.1 \pm 5.0 [5.3-26.6]	10.0 \pm 4.3 [4.5-23.2]	6 cm s^{-1}
<i>O. melanura</i>	1	13.1	13.7	
<i>S. smarís</i>	31	13.1 \pm 6.2 [7.2-26.6]	11.4 \pm 4.4 [5.5-22.4]	
<i>D. annularis</i>	26	11.6 \pm 5.1 [6.1-20.9]	11.5 \pm 5.4 [7.0-23.2]	
<i>B. boops</i>	40	9.4 \pm 3.2 [5.3-25.3]	8.4 \pm 3.1 [4.5-22.6]	
Fastest larva	1	37.4	30.4	19 cm s^{-1}
Slowest larva	1	5.3	4.5	2.5 cm s^{-1}

mented and seemingly less developed than those of the large sparids group (Figure 6.2). When swimming speeds were pooled across species within each group, large sparids were found to swim significantly faster than small sparids (Wilcoxon, $p < 0.001$).

When swimming speed was standardised by body-length to account for large differences in size among species, Mugilidae sp. and *C. chromis* had similar U_{crit} (ca. 24 BL s^{-1} ; pairwise-Wilcoxon, $p = 0.66$). Likewise, the Sparidae *S. cantharus*, *S. smaris* and *D. annularis* shared comparable U_{crit} (14.8 BL s^{-1} , 11.5 BL s^{-1} and 11.5 BL s^{-1} respectively; pairwise-Wilcoxon, all $p > 0.05$). Other Sparidae in which only one individual was tested presented swimming speeds in the same range: from 10.7 to 14.4 BL s^{-1} . While body length therefore seemed to account for some differences between species, within species, critical swimming speed was never influenced by body length (linear regression, all $p > 0.05$).

Mugilidae sp., *C. chromis* and large sparids all swam in an inertial regime ($Re > 1000$), where swimming is easier and more energy efficient (Figure 6.4). Small sparids were evenly split between $Re < 1000$ and $Re > 1000$. Therefore, some small sparids swam in a more viscous regime. The biggest larvae did not systematically swim in high Re environments.

6.3.2 Modeling experiment

The overall proportion of successful settlers increased from 8.7% for passive larvae, to almost twice as much for the slowest virtual larvae, swimming at 2.5 cm s^{-1} (16.1%; Figure 6.5). Over half of virtual Pomacentridae larvae, swimming at 12 cm s^{-1} , settled successfully (51.1%). This percentage rose to 70% for the fastest Mugilidae sp., swimming at 19 cm s^{-1} . Settlement rate increased completely linearly with swimming speed ($F = 2191$, $R^2 = 0.99$, $p < 0.001$; Figure 6.5).

In all simulations, the probability of settling within the four days of simulation was high almost everywhere along the coast and decreased offshore, representing the simple fact that reaching the coast is easier when starting close to it (Figure 6.6). However, swimming speed influenced the distance from which reaching the coast was possible. For example, no passive larvae starting further than 10 km offshore could settle. In contrast, the fastest larvae could settle from anywhere in the domain (settlement probability always > 0 , albeit very small in some locations; Figure 6.6). More quantitatively, the isoline of settlement probability = 0.5 was located at 5 km from the coast on average for passive larvae, while it was at 21 km for small sparids (swimming speed = 6 cm s^{-1}), at 43 km for *C. chromis* (swimming

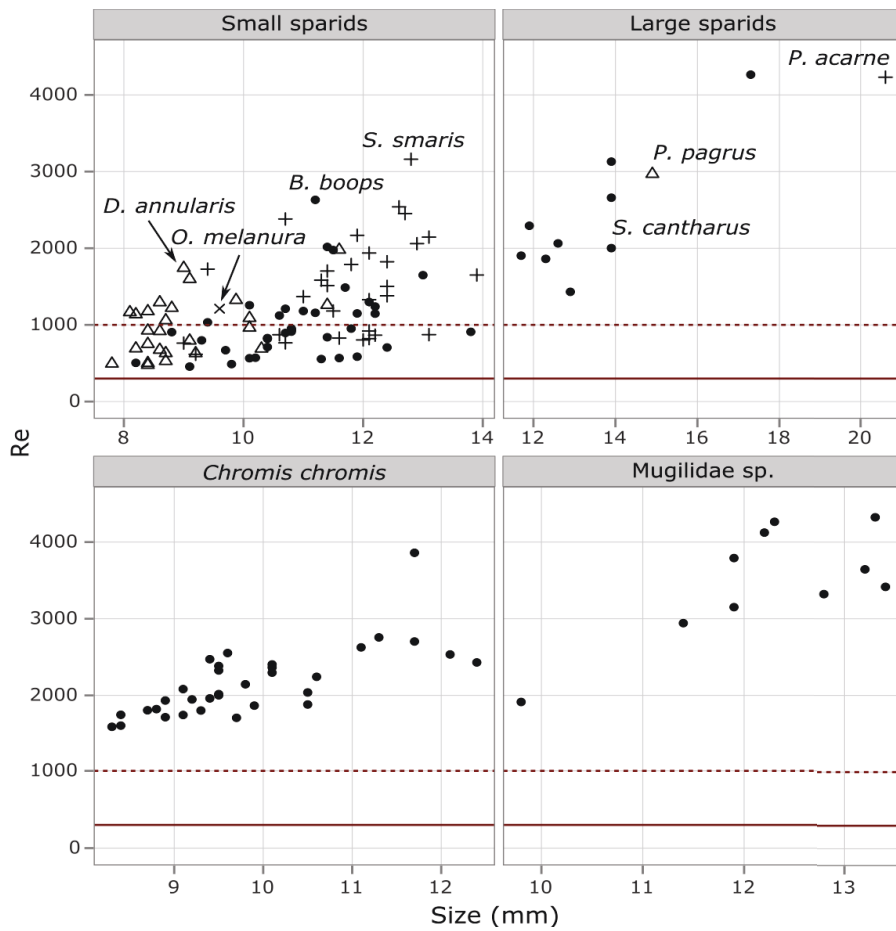


Figure 6.4: Reynolds number (Re) for each larva as a function of standard length (SL). Species are identified by symbols within each panel. The swimming environment would be viscous below the solid line ($Re < 300$) and inertial above the dotted one ($Re > 1000$).

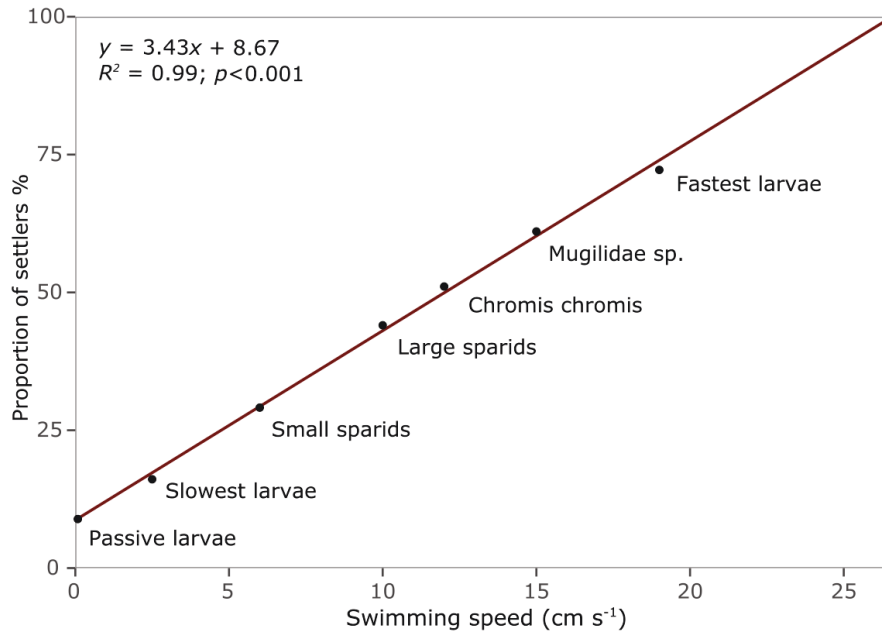


Figure 6.5: **Relationship between the proportion of settlers and swimming speed of virtual larvae.** Each point corresponds to one simulation scenario and is computed from about 2 million virtual larvae. The line represents the result of a linear regression ($R^2_{adj}=0.99$; $p<0.001$).

speed = 12 cm s⁻¹) and at 56 km for the fastest Mugilidae sp. (swimming speed = 19 cm s⁻¹).

Some coastal features such as the Hyères Peninsula, the Bay of St-Tropez and the Cape of Antibes (Figure 6.6) acted as retention areas, in particular for passively drifting particles that displayed higher settlement probability than in other coastal areas. At mesoscale, the two main eddies (Figure 6.1) drove similar patterns in all simulations (Figure 6.6). On the southwestern boundary of the (southern) anticyclonic eddy, as well as on the northeastern boundary of the (northern) cyclonic eddy, water flowed towards the continent hence facilitating the transport of virtual larvae to settlement sites and extending offshore the zones of high settlement probability. Conversely, along the eastern boundary of the anticyclonic eddy, water flowed towards Corsica, also offering opportunities for successfully reaching a coast. Finally, a zone of low settlement probability close to the shore (in the northeastern corner of the domain) was created by the northern cyclonic eddy, which quickly carried virtual larvae away from the shore, making it more difficult to come back to the coast and settle within the four days of simulation.

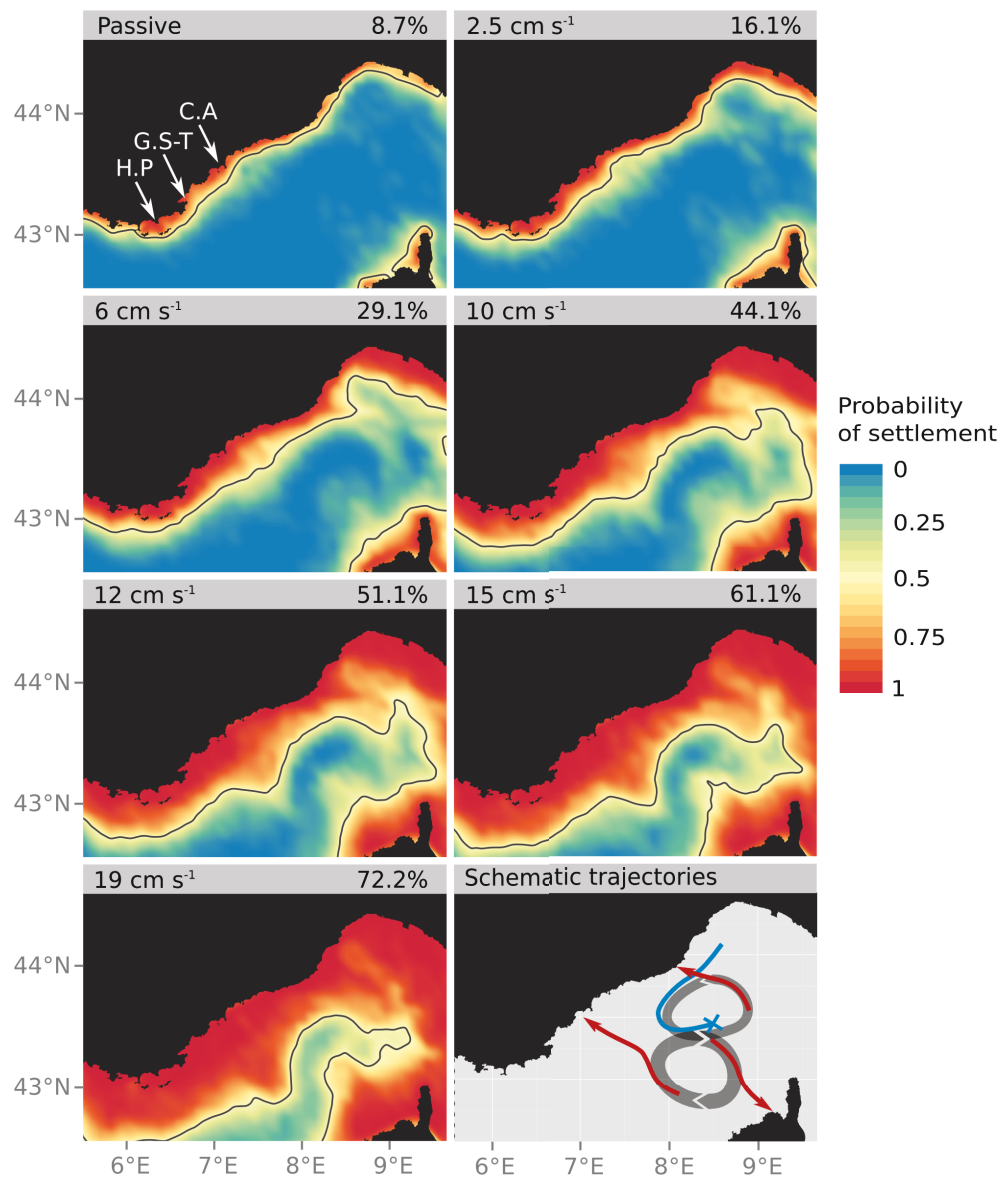


Figure 6.6: Maps of the probability of settlement on the coast of fish larvae released over the whole domain, for seven simulation scenarios. For each simulation, the swimming speed of larvae and percentage of successful settlers are indicated above the map. The isoline of settlement probability = 0.5 is drawn in grey. Coastal features acting as retention areas are indicated on the passive simulation map (C.A: Cape of Antibes, G.S-T: Gulf of Saint-Tropez, H.P: Hyeres Peninsula). The bottom-right panel shows the effect of the two mesoscale eddies on larval transport, with arrows representing schematic larval fish trajectories (red: successfully settled; blue: still offshore at the end of the simulation).

6.4 DISCUSSION

6.4.1 *Swimming performance of Mediterranean settlement-stage fish larvae*

Comparison with other studies

The critical swimming speeds measured here were surprisingly high for temperate fish larvae, which were usually found to be slower than tropical species [100, 114]. Mugilidae sp. and *C. chromis* swam particularly fast, at more than 20 cm s⁻¹ on average; Sparidae were slightly slower.

Swimming speed of Mugilidae have been reported in a few studies, with a maximum swimming speed (equivalent to U_{crit}) of 40 cm s⁻¹ or 12.7 BL s⁻¹. But those were juveniles (measuring ~30-40 mm in standard length) [322, 323]. The larvae studied here were about 12 mm in standard length but their critical speeds were already remarkable (U_{crit} =29.2 cm s⁻¹ or 24 BL s⁻¹). This confirms that young Mugilidae are very proficient swimmers, at least around the settlement period.

Numerous studies have been focused on tropical pomacentrids (e.g. Fisher *et al.* [306] summarised swimming speeds of 28 species). *Chromis chromis* (U_{crit} =24 cm s⁻¹ or 24 BL s⁻¹) swam slower than the average tropical pomacentrid (U_{crit} =37.6 cm s⁻¹ or 30 BL s⁻¹) but was also slightly smaller (SL=9.9 mm vs. 12.5 mm). In addition, five tropical species had U_{crit} lower than *C. chromis*, so this only representative of the family Pomacentridae in the Mediterranean is well within the range reported for the family elsewhere.

Within the family Sparidae, two groups seemed to be distinguishable in this study based on their swimming speeds and morphology: small, slender bodied larvae (*B. boops*, *D. annularis*, *S. smaris* and *O. melanura*) and large, muscular larvae (*S. cantharus*, *P. pagrus*, *P. acarne* and *D. dentex*). Yet, for three of the four large sparids, there is only data on one individual per species. Since variability in performance is usually high [e.g. 289, 301, 306], caution should be taken regarding these results. Nevertheless, the two groups identified also have different pelagic larval duration, as the large sparids is longer (30-38 days) than the one of the small sparids (16-18 days [232]), suggesting that the morphological differences observed indeed reflect differences in the advancement of their development. The settlement-stage larvae of *Sparus aurata* could fit in the small-sparids group: at 10 mm, their critical speed was measured at 11.4 cm s⁻¹ by Faria *et al.* [303]. The species is present in the Mediterranean Sea but those measurements were done in the Atlantic Ocean, off the coast of Portugal. *Pagrus auratus*, another temperate but non-Mediterranean species, dis-

played similar sizes and critical speeds at settlement: $SL=9-10$ mm and $U_{crit}=10-15$ cm s^{-1} [301]. Compared to the large-sparids group, the settlement-stage larvae of *Sarpa salpa*, in South Africa, displayed similar characteristics ($SL=15.6$ mm [291], pelagic larval duration = 29-35 days [232]) and critical speed ($U_{crit}=18.0$ cm s^{-1} [291]). These comparisons suggest that the morphological/developmental differences noticed here might hold some generality in the Sparidae family.

Overall, those speeds were always comparable to and often larger than, average coastal currents speed in the region (for example, the average of the output of the MARS3D model over June 2014 within ~15 km of the coast was 13 cm s^{-1}). The settlement-stages of these species are therefore “efficient swimmers” (*sensu* Leis [100]) and should certainly be categorised as nekton rather than plankton.

Reynolds number

Efficient swimming can also be defined in terms of energetic expenditure. Temperate fish larvae are assumed to swim in a more viscous environment than tropical ones [100]: they are smaller, swim slower and the water is colder, all contributing to a lower Reynolds number (Re). Most larvae tested here actually swam in an inertial, energy-efficient environment ($Re>1000$ [314]). The few small-sparids larvae which displayed $Re<1000$ were still out of the most energetically-costly viscous environment ($Re>300$). The differences in swimming speed and swimming regime between tropical and warm-temperate larvae seem therefore small, at least for these species.

Inter-individual variability

In most species, the fastest individual was at least 1.3 times faster, often 2 times faster than the average of the species (Table 6.2). These large inter-individual differences in critical swimming speed within species have been commonly observed [e.g. 289, 301, 306]. Mortality of fish larvae can be huge (up to $>70\%$ day^{-1} [15]) and selective, so only the best performers may matter [324], since they are likely the only ones that survive and contribute to the replenishment of adult populations. It would therefore be important to know what drives variations between individuals. Johnson *et al.* [324] examined size, but size never explained differences in swimming speeds within species here. Other factors could be investigated such as body shape, symmetry (possibly assessed on otoliths), muscle mass, or condition [100, 303, 325]. This variability also puts in perspective the speeds measured on only one individual here. They allow gaging size orders but replicated measurements are definitely necessary before using them for anything else.

Influence of morphology

Size did explain differences in swimming speed between species. Critical speeds in BL s^{-1} were comparable for all Sparidae but speeds in $cm s^{-1}$ were not, indicating that these species have similar swimming efficiency but different sizes. Mugilidae sp. and *C. chromis* were also comparable to each other and faster than Sparidae. These two species have the most ontogenetically-advanced appearance: very pigmented and muscular body, well defined fin spines and rays, etc. (Figure 6.2). These observations, together with the differences between the two groups of Sparidae presented earlier, are in adequation with previous observations as they suggest that similarities in the developmental stage and morphology of fish larvae would be better predictors of swimming abilities than taxonomical relatedness [326]. For modeling purposes, generalisations based on taxonomy alone should be avoided, such as using U_{crit} in $cm s^{-1}$ from another species in the family when data is lacking for the species of interest. Estimating swimming speed in BL s^{-1} would lessen some of these concerns.

6.4.2 *Why larval fish swimming abilities nuance Hjort's aberrant drift hypothesis*

Hypotheses of the model

The simulations highlighted that swimming abilities of fish larvae considerably increased settlement, even over just the few days of their competency period. They also showed that the proportion of settlement increased completely linearly with swimming speed. In our model, virtual larvae swam continuously for four days, at the same speed, in the same somewhat stochastic but still oriented manner, with no mortality, near the surface and with no vertical migration.

In the ocean, the swimming behaviour of larvae is likely to vary, at least between day and night and depending on food density [100]; but these patterns are very under-documented. They are not incompatible with this study, because we used equivalent *in situ* speed, which is a speed at which larvae have been observed to feed [253, 308]. Thus, this speed averages slow down during foraging events and higher speeds in between. As already explained, *in situ* speed does not measure forced swimming performance but the natural pace of larvae in their environment and is likely to be sustainable over very long periods [100]. Swimming endurance of larvae fed during the experiment was measured only once [298]. For tropical Pomacentridae swimming at $13.5 cm s^{-1}$, it was 5.5 days on average and it exceeded four days for five species out of six tested. Average U_{crit} ranged between 25 and $49 cm s^{-1}$ for these species [306], so they were swimming below half

of their U_{crit} ($0.4 \times U_{\text{crit}}$ on average) while our simulated larvae swam slightly faster, at $0.5 \times U_{\text{crit}}$. Still, it seems quite reasonable that the *in situ* speed used in the model could be sustained for the four simulated days. In addition, most successful settlers reached the coast before the very end of the simulation and therefore swam less than four days.

The accuracy of orientation over large spatial scales remains fundamentally unknown for fish larvae, although increasing evidence converges towards the existence of coast-independent cues, such as sun position that fish larvae might use as a compass to orient in the open ocean [116, 124, 274]. As shown in Chapter 5, open-ocean orientation was investigated for four of the species tested here, in the same location and three exhibited behaviour consistent with the existence of a sun-compass.

Mortality over the few last days of the pelagic larval phase would decrease the observed proportion of settlement, but only constant mortality rates could have been included in the model (because nothing is known regarding the spatial heterogeneity of mortality rates). Constant mortality would not have altered the spatial patterns discussed in this paper.

Finally, virtual larvae were simulated near the surface because larvae of Sparidae and Mugilidae (9 of the 10 tested species) are mostly concentrated in the upper 10 m of the water column and show very limited diel vertical migration in the Mediterranean Sea [105, 327]. This is also consistent with the vertical distributions observed in Chapter 2.

So, overall, while this model was clearly meant to represent a higher bound of the influence of directional swimming on dispersal trajectories, to be contrasted with mostly passive simulations, its configuration was still based on realistic assumptions.

Limited influence of hydrological structures

One important result of this study was the absence of thresholds or asymptote in the relationship between swimming speed and proportion of settlers, at least within the range of values tested. A substantial change would have been expected between purely passive particles and larvae swimming directionally, at any swimming speed [89, 275]. Also, the Ligurian current is known to create a barrier to passive coastal particles [148], thus only larvae swimming fast enough, above a threshold speed, should have been able to cross it. Finally, the relationship should reach an asymptotic maximum settlement rate lower than 100%, as some larvae may irremediably be lost outside of the domain for example, no matter their swimming speed. The strictly

linear relationship observed between swimming speed and proportion of settlers refutes all of these expectations. It suggests that, for late-stage larvae, distance from the coast is actually the variable that most limits settlement and that directional swimming at any pace helps with getting closer to the shore. It also shows that the effect of the along-shore Ligurian current as a barrier to passive organisms is negated by even limited shoreward (i.e. cross-current) swimming.

Hjort's hypothesis and larval behaviour

While the effect of the Ligurian current was weak, some retention areas were still present along the coast. Some mesoscale eddies also significantly contributed to shoreward transport (Figure 6.6). Still, larvae drifting passively and ending further than 5-10 km offshore at the start of their competency period had very low probability to settle. In Hjort's terminology, those larvae would be *aberrant drifters* and would not survive. Such drift is likely to occur in many of the species studied here, since most Sparidae and Mugilidae spawn offshore pelagic eggs that may drift away from shore during their early pelagic phase. Yet, considering larval behaviour creates a very different picture, as those seemingly *aberrant drifters* would actually have a non-negligible probability to settle if they swim actively during their last few days as larvae. These results have major implications for predicting fish larvae settlement. They also open the possibility of various trade-offs during the larval phase: young fish larvae may allocate most of their energy to growth, hence diminishing mortality by limiting predation and starvation [15] and only start swimming towards the coast once competent, when they are efficient swimmers. Young fish larvae could still have considerable influence over their dispersal trajectories, by actively staying close to the shore [275] or swimming down to avoid strong surface currents and favor retention [93]. Nevertheless, even if they do drift away, the present model shows that their swimming abilities at a later stage provide them with the means to overcome aberrant drift.

6.5 ACKNOWLEDGMENTS

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DISCUSSION GÉNÉRALE

Les objectifs de ce travail étaient de collecter des données sur le comportement des larves de Perciformes de Mer Méditerranée, puis de déterminer l'importance potentielle de ces comportements sur la dispersion (et en moindre mesure sur la survie) des larves de poissons au cours de leur phase pélagique. De plus, peu d'informations étaient publiées sur les larves de poissons de cette région avant le début de ce travail.

7.1 PRINCIPAUX RÉSULTATS DE LA THÈSE

Le Chapitre 2 présente une description de la distribution de l'ichtyoplancton le long d'un transect côte-large à travers le front généré par le courant Liguro-Provençal, à partir de prélèvements de filets à plancton et d'imagerie *in situ*. La distribution de l'ichtyoplancton y est sensiblement distincte de celle observée au niveau des autres fronts de Méditerranée Nord-Occidentale, notamment par la présence d'un unique assemblage larvaire situé du côté côtier du front, composé d'espèces côtières, pélagiques et mesopélagiques. Leur distribution à fine échelle met en évidence la présence d'agrégations en surface, parfois très denses, d'un comportement de migration nycthémerale d'amplitude limitée et suggère l'existence d'un comportement d'évitement des prédateurs zooplanctoniques à micro-échelle.

La méthode d'imagerie utilisée dans le Chapitre 2 génère de très grandes quantités de données. Nous avons repris les données collectées et identifiées manuellement pour développer une méthode d'automatisation du traitement de données d'imagerie dans le Chapitre 3. Cette méthode a notamment permis de prédire correctement la distribution horizontale et verticale d'une dizaine de taxa planctoniques en utilisant seulement 0,41% des données validées pour prédire le reste. Cette méthode est adaptée pour l'étude de la distribution des proies, compétiteurs ou prédateurs zooplanctoniques des larves de poissons. Cependant, les larves de poissons restent difficiles à traiter de façon automatique du fait de leur similarité avec les appendiculaires. Les larves de poissons et les appendiculaires peuvent donc être isolés dans même groupe automatiquement, mais ils devront être différenciés l'un de l'autre manuellement.

Les capacités comportementales des larves de poissons tropicaux sont maximales à la fin de leur phase pélagique. Afin d'estimer si

A single larval fish assemblage before the Ligurian front

Fish larvae aggregate at the surface and avoid predators at microscale

Automatic prediction of plankton distribution patterns is possible

But fish larvae are particularly hard to predict

Fish larvae settlement is seasonal ...

... and related to the moon phase

Fish larvae use to sun as a coast-independent cue for orientation

They have strong swimming abilities ...

... to the point that aberrant drift is unlikely in these species

cela se confirme en milieu tempéré, il était nécessaire de collecter des larves en phase d'installation. Nous avons donc mis en place un suivi hebdomadaire de leur arrivée à la côte. Sur les trois premières années d'échantillonnage, cela a permis de mettre en avant des patrons de saisonnalité marqués [Chapitre 4]. Des échantillonnages à plus fine échelle temporelle suggèrent une synchronisation très marquée avec la phase de la lune, la plupart des larves s'installant pendant les heures de la nuit les plus sombres et principalement entre le dernier quartier et la nouvelle lune. Couplée à un possible comportement grégaire, cette synchronisation pourrait également traduire une stratégie d'évitement de prédateurs.

Le Chapitre 5 a révélé que les larves en phase d'installation étaient capables de s'orienter par rapport au soleil, fournissant la première preuve *in situ* d'un mécanisme d'orientation à large échelle chez des larves de poissons [Chapitre 5].

En parallèle, les expériences en laboratoire présentées dans le Chapitre 6 ont montré que ces mêmes larves possédaient des capacités de nages non-négligeables, allant d'une dizaine de centimètres par seconde à une quarantaine pour les plus rapides. La prise en compte de ces capacités comportementales dans un modèle biophysique d'advection lagrangienne, reproduisant les conditions hydrodynamiques pendant leur période d'installation, a mis en évidence le potentiel des larves à influencer leur dispersion. Les larves pourraient donc rejoindre la côte à la fin de leur phase pélagique grâce à leurs capacités de nage, au point de nuancer les concepts de dérive aberrante de Hjort [1] et de rétention stable de Sinclair [26, 27].

7.2 DESCRIPTION DU CYCLE DE VIE DES POISSONS DÉMERSAUX EN MER LIGURE

En Méditerranée, la reproduction des espèces de poissons a lieu majoritairement au printemps et en été [223, 328] et semble liée à la stratification de la colonne d'eau ainsi qu'à la biomasse de phytoplancton et zooplancton [152]. La série temporelle de l'arrivée des larves à la côte semble confirmer l'influence des conditions environnementales spécifiques sur la reproduction des adultes. En particulier, nous avons observé que le pic d'arrivée des larves à la côte était synchronisé, selon un délai constant, avec les pics des blooms printaniers de phyto- et zooplancton [Chapitre 4]. Toutefois, le délai entre les blooms planctoniques et le pic d'arrivée des larves de poissons implique qu'ils ne se chevauchent pas temporellement. Cela suggère que les poissons favoriseraient les conditions post-blooms pour se reproduire, à savoir des abondances de proies plus faibles que lors des blooms, mais des températures en augmentation.

Fish larvae are more abundant after the bloom ...

Par ailleurs, après avoir localisé un patch, les larves de poissons sont capables d'adapter leur comportement pour se maintenir au sein de celui-ci et de se nourrir à une haute intensité [329]. En conséquence, les larves de Sparidae ont le même taux de survie qu'elles soient en présence de patchs de proies tout au long de la journée ou pendant trois heures seulement [330]. Cela suggère que leur comportement leur permettrait de s'adapter aux variations de densité de proies pour maximiser leur taux de nutrition dès lors que des proies sont présentes. Ainsi, les larves de poissons devraient être capables de se nourrir à des taux relativement élevés même lorsque leurs proies sont plutôt rares, mais concentrées en patchs en permanence ou pendant une partie de la journée seulement (e.g. au niveau de la thermocline le jour ou en surface la nuit).

... but their feeding behaviour may compensate the oligotrophy ...

De plus, les larves de poissons seraient capables de s'alimenter sur du microzooplancton [331] et autres produits de la boucle microbienne en milieu oligotrophe (synthétisé dans [126]). Les larves seraient donc susceptibles d'exploiter l'ensemble des ressources disponibles dans la colonne d'eau. Elles seraient donc capables de se nourrir même lorsque leurs proies "traditionnelles" (e.g. copépodites et copépodes) sont peu abondantes, voire absentes, même en milieu oligotrophe [332].

... and they could feed on various types of prey

La stratégie de ponte diffère entre les espèces de poissons démersaux, certaines pondant des œufs pélagiques (e.g. les familles Seranidae, Scorpaenidae, Triglidae) et d'autres déposant des œufs benthiques (e.g. les familles Apogonidae, Pomacentridae, Blenniidae). Toutefois, en accord avec [256], la distribution des larves collectées au large suggère que la dispersion vers le large des stades pélagiques de

Larvae of both benthic and pelagic spawning species disperse offshore

ces espèces serait peu influencée par leur stratégie de ponte, puisque des espèces côtières suivant les deux stratégies ont été collectées jusqu'à plus de 20 km au large. Les stades pélagiques des espèces démersales de Mer Ligure sont donc susceptibles de dériver assez rapidement jusqu'à plusieurs dizaines de kilomètres vers le large.

The frontal zone seems most favourable for survival

La distribution des larves par rapport au front Ligure peut influencer leur dispersion et leur survie. En effet, si les larves dérivent jusqu'à la zone centrale, leur éloignement par rapport à la côte et les faibles abondances de proies leur seront plutôt défavorables, mais les prédateurs y sont peu abondants. Au contraire, la zone frontale sert de nurserie pour plusieurs espèces de copépodes [145], dont les nauplii et copépodites sont une source importante de nourriture pour les larves de poissons [106, 164, 333, 334]. De plus, les groupes zooplanctoniques prédateurs de larves de poissons ne semblent pas s'y accumuler [Chapitre 2], bien que des adultes de *Pelagia noctiluca* y soient régulièrement observés [335]. La zone frontale serait donc favorable à une croissance rapide. Cependant, le fort courant parallèle à la côte qui la caractérise engendrera un transport important (20 à 40 km par jour). Enfin, dans la zone périphérique (du côté côtier du front), des proies potentielles sont également disponibles et les courants y sont plus variables et moins forts que dans la zone frontale [174, 312], pouvant favoriser la rétention des larves à proximité de leurs zones de nurseries [148]. Cependant, la zone périphérique est aussi la zone où les prédateurs sont les plus abondants, augmentant le risque de mortalité par prédation.

However, fish larvae are more abundant in the peripheral zone ...

Les observations du Chapitre 2 indiquent que les larves de poissons côtiers sont principalement distribuées dans les zones de faible courant, où la densité de prédateurs est élevée. Cependant, les larves de poissons seraient capables d'éviter les zones de forte abondance de prédateurs à micro-échelle [Chapitre 2]. Ainsi, nous pouvons supposer que l'hydrodynamisme local évite aux larves de poissons de dériver au-delà de la zone frontale, tandis que leur comportement permettrait d'optimiser leur environnement immédiat (densité de proies, de prédateurs, température, etc.).

... but may be able to optimise their local environment

Après cette phase pélagique, les larves d'espèces côtières s'installent à la côte. En 2013, nous avons des informations à la fois sur leur présence au large [Chapitre 2] et sur leur installation [Chapitre 4]. La chronologie est compatible pour la majorité des espèces. Par exemple, les Triglidae et *C. chromis* ont une phase pélagique relativement courte (<19 jours [232]). Ils ont été observés pendant le mois de juillet au large et rapidement ensuite, avant la fin de ce même mois, à la côte. Les Blenniidae et Scorpaenidae ont une phase pélagique plus longue (≥ 30 jours [232, 241]) et ont été principalement capturés en août, après la campagne de juillet. *Apogon imberbis* est la seule espèce pour

laquelle la chronologie n'est pas complètement compatible, puisque les premiers individus ont été collectés à la côte près de six semaines après que l'espèce ait été observée au large, alors que sa phase pélagique ne dure que trois semaines [232, 241]. Ainsi, il est probable que, à cette exception près, les larves capturées à la côte durant l'été 2013 proviennent des cohortes observées au large qui auraient réussi à rejoindre la côte. Il est également intéressant de noter qu'en juillet 2013, la saison de reproduction des Sparidae était probablement déjà terminée au moment de la campagne. En effet, aucune larve n'a été collectée pendant celle-ci ou au niveau des habitats d'installation de mi-juillet à fin août.

Cohorts observed offshore were caught again when settling

Par ailleurs, les données présentées dans ce travail ont permis de décrire les patrons saisonniers d'arrivée de larves à la côte [Chapitre 4], ainsi que les fluctuations mensuelles qui ont été mises en relation avec la phase de la lune. Cependant, elles n'expliquent pas la variabilité interannuelle, à savoir que le flux de larves a été deux fois supérieur pendant la période estivale de 2014 par rapport à 2013 et 2015. Les causes pourraient donc être à chercher auprès de facteurs agissant à plus large échelle, notamment la variabilité de l'habitat pélagique.

Hydrological conditions did not explain settlement intensity ...

La distribution des larves de poissons en Mer Ligure est principalement structurée par la position du courant Liguro-Provençal [Chapitre 2]. La structuration de cette zone frontale dépend d'une part de la température, qui va déterminer la stratification des couches de surface, et d'autre part de l'intensité du courant [172]. De plus, le courant se situe généralement plus proche de la côte lorsque son énergie est élevée [174] alors qu'un courant plus faible engendre une zone frontale plus diffuse, avec des cellules obliques de circulations plus réduites et plus éloignées de la côte. Cela aurait pour conséquence de réduire la rétention d'organismes passifs dans les zones périphériques et frontales [148]. Or, au cours des mois de mai à juillet, soit pendant la période de plus forte abondance de larves, l'intensité du courant dans les zones périphérique et frontale était plus élevée en 2014 qu'en 2013 et 2015 (Figure 7.1). Cela indiquerait que l'hydrodynamisme était plus important en 2014 et que les cellules de convergences et divergences qui en résultent pourraient avoir favorisé la rétention et la survie des larves à leur phase pélagique. La pérennisation du suivi de l'arrivée des larves au cours des prochaines années devrait permettre de préciser l'existence d'une relation entre l'intensité et la position du courant Liguro-Provençal et l'intensité du flux d'arrivée des larves à la côte.

... but it may be related to the Ligurian current intensity ...

Un autre facteur à prendre en compte pourrait être l'abondance de macroprédateurs gélatineux dans le milieu pélagique, puisqu'ils

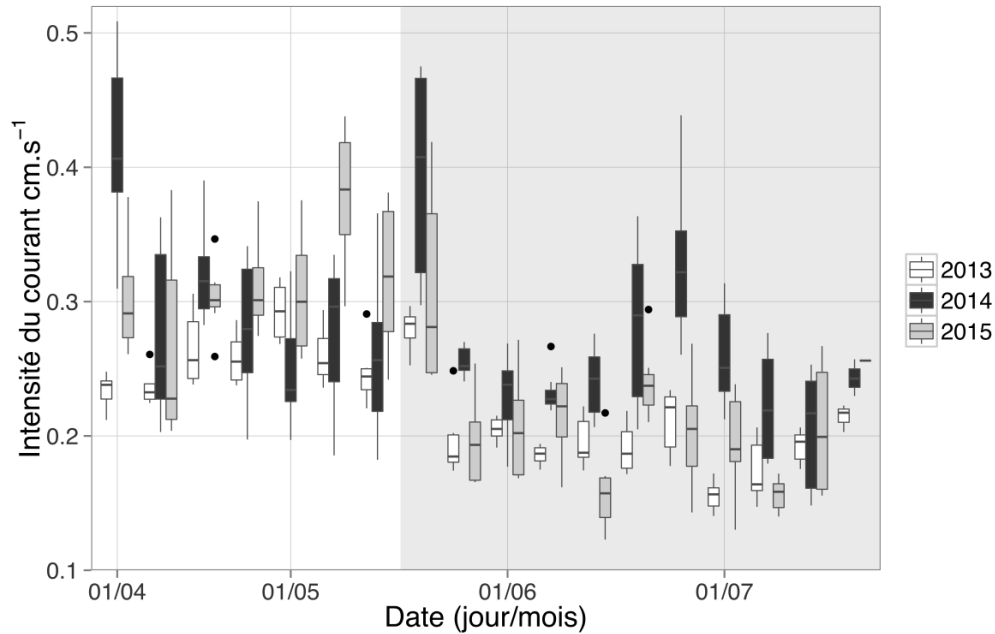


FIGURE 7.1 : **Intensité du courant dans les zones périphérique et frontale au cours de la période de reproduction des poissons démersaux (avril à juillet) de 2013 à 2015.** La période correspondant aux abondances les plus élevées est représentée en gris clair. La vitesse du courant a été calculée entre la surface et 150 m de profondeur, toutes les semaines à partir des sorties du modèle MARS3DMED (présenté dans le Chapitre 6). La zone de calcul commence à 5 km au large de la côte et s'étend jusqu'à la position moyenne du front séparant la zone frontale de la zone centrale (~40 km de la côte [Chapitre 2 ; 174]), entre Imperia, Italie, et Toulon, France.

peuvent se nourrir d'œufs et de larves de poissons, au point de limiter le repeuplement des stocks d'adultes [336]. En Mer Ligure, le cténophore *Mnemiopsis leidyi* est fréquemment observé depuis 2009 [337] et les densités de scyphoméduses *P. noctiluca* y atteignent régulièrement plus d'un individu adulte par m² [335].

En se basant sur le peu de données disponibles, il semble que les variations interannuelles des flux d'arrivée de larves à la côte soient anticorrélées avec les abondances de ces macroprédateurs gélatineux (Figure 7.2). En effet, en 2014, très peu de méduses ont été observées au large pendant la période de reproduction des poissons, alors qu'elles étaient très abondantes en 2013 et 2015 (Figure 7.2). L'abondance de cténophores *M. leidyi* dans la baie de Villefranche a suivi la même tendance : alors qu'ils étaient absents en 2014, ils étaient présents en continu pendant l'été 2013 et 2015, avec notamment un

... or the abundance
of gelatinous
macropredators

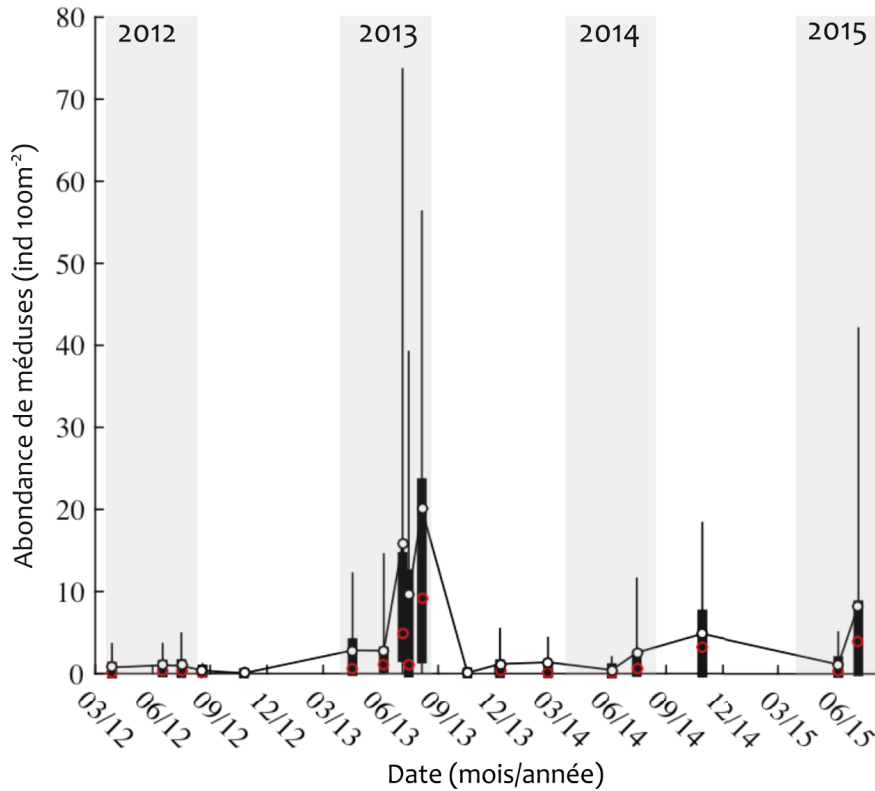


FIGURE 7.2 : Abondance moyenne (points blancs), médiane (points rouges) et quantiles 95% (rectangles noirs) de *P. noctiluca* de nuit dans les eaux de surface à travers le courant Liguro-Provençal, le long du même transect que celui effectué pendant la campagne présentée dans le Chapitre 2. Les rectangles grisés indiquent la saison de reproduction de la majorité des espèces de poissons démersaux en Méditerranée (avril à août) [F. Lombard et M. Lilley., pers. comm.].

bloom de plusieurs individus par m² au début de l'été 2013 [F. Lombard et M. Lilley., pers. comm.].

Ces observations suggèrent que la variabilité interannuelle de l'habitat pélagique pourrait être un facteur important pour le succès de la survie des larves de poissons à leur phase larvaire pélagique. Le suivi de l'abondance des prédateurs gélatineux, de la dynamique du courant Liguro-Provençal et de l'arrivée des larves de poissons à la côte continuera. Ainsi, une analyse quantitative avec davantage de données permettra de confirmer ou d'infirmer les hypothèses de contrôle du repeuplement des populations de poissons dans la région par la position du courant et/ou l'abondance de macrozooplancton gélatineux.

Correlation between the pelagic habitat and settlement intensity will be further explored

7.3 MODÉLISATION DE LA DISPERSION DES LARVES DE POISSONS : QUELLE INFLUENCE DU COMPORTEMENT LARVAIRE ?

7.3.1 *Le comportement larvaire dans les modèles biophysiques : focus sur la Méditerranée*

L'utilisation de modèles couplant biologie et physique a fortement contribué à la compréhension et à la description de la dispersion larvaire, notamment dans le but de prédire le recrutement dans les populations adultes [321]. Il existe désormais des preuves certaines de l'importance des capacités comportementales des larves de poissons, au moins pendant leur phase d'installation [Chapitres 5 et 6 ; 100, 122, 263] et, pour certaines espèces, au cours de l'ontogénie [16, 100]. L'hypothèse simplificatrice ("Simplifying assumption" *sensu* Leis [100]) qui consiste à considérer les comportements larvaires comme négligeables par rapport aux courants marins n'est pas applicable pour les larves d'espèces de Perciformes [228].

Behaviour should be implemented in larval fish dispersal models

Depuis quelques années, plusieurs articles de synthèse insistent sur l'importance de prendre en compte des comportements larvaires réalistes dans les modèles de dispersion [115, 269, 321, 338]. Par exemple, Leis [338] liste 14 conseils à suivre pour l'incorporation du comportement larvaire afin de produire des modèles de connectivité plus réalistes. Ses principales recommandations sont d'utiliser des données empiriques, collectées sur l'espèce testée et non des espèces taxonomiquement proches, mais aussi de représenter les changements du comportement au cours de l'ontogénie. Pourtant, de récentes études considèrent encore que les larves de poissons dérivent de façon passive [e.g. 339] ou ne considèrent qu'un seul comportement, celui de migration verticale [e.g. 340].

In the Mediterranean, most models omit larval fish behaviour

En Méditerranée en particulier, Di Franco *et al.* [341, 342] ne modélisent pas de comportement, mais utilisent l'approche de modélisation en complément d'études empiriques afin d'estimer la distance maximale de dispersion des particules. Koeck *et al.* [343] n'incluent pas non plus de comportement dans leur modèle, mais cherchent à décrire l'export potentiel de propagules depuis une aire marine protégée. Or, les jeunes stades de développement pouvant effectivement être considérés comme passifs, l'export initial au moins pourrait être correctement représenté [338]. Cependant, le comportement des larves pourrait complètement brouiller ces patrons d'export initiaux ainsi que ceux à la fin de leur phase pélagique [Chapitre 6]. Andrello *et al.* [340] cherchent explicitement à estimer la connectivité entre les aires marines protégées existantes en Mer Méditerranée et prennent comme espèce modèle le mérrou brun (*Epinephelus marginatus*). Deux

configurations sont testées, une principale avec des larves passives, une seconde avec de la migration verticale entre 0,2 m la nuit et 50 m le jour pendant toute la phase de dispersion. Dans les deux cas, ils obtiennent des distances moyennes de connexions supérieures à 100 km ; la prise en compte des migrations verticales ne diminuerait que très légèrement les distances de connectivité.

Basterretxea *et al.* [344] modélisent également la connectivité à partir d'une aire marine protégée à Majorque en ne prenant en compte aucun comportement. Ils observent un taux de rétention dans les 10 km autour de la côte atteignant 30%, qui dépend de l'intensité du vent. Cependant, du comportement est implémenté dans un second modèle [345] : les larves nagent vers la côte à 5 cm s^{-1} , de façon continue ou uniquement lorsque les courants les en éloignent. Les deux stratégies fournissent des résultats similaires : 41% de larves retenues à <10 km de la côte lorsque la nage est continue contre 37% pour la nage uniquement en cas d'éloignement vers le large. Cependant, le coût énergétique associé à la nage est largement réduit dans le second cas (46% du temps en nage).

Le dernier exemple et le Chapitre 6 de cette thèse sont des exceptions en Méditerranée et montrent que du chemin reste à parcourir pour que le comportement des organismes biologiques simulés soit effectivement représenté dans les modèles de transport et de connectivité larvaire.

Nous suggérons que les modèles qui n'intègrent pas le comportement des organismes biologiques simulés omettent un processus majeur qui pourrait changer de façon importante leurs prédictions. Pourtant ces modèles restent la règle, plutôt que l'exception. Se pose alors la question de leur validité et de la magnitude des changements qui peuvent être attendus lorsque le comportement est intégré.

Le Chapitre 6 montre que la prise en compte du comportement de nage orientée dans un modèle focalisé uniquement sur les derniers jours de la vie larvaire cause déjà des changements importants dans les taux d'arrivée à la côte et les zones considérées comme favorables à l'installation. Mais cet exercice de modélisation ne pose pas directement des questions de connectivité et n'intègre qu'un aspect du comportement des larves de poissons. L'objectif de la partie suivante est d'aller un peu plus loin : donner un exemple quantitatif de l'influence de l'ensemble des comportements observés ou inférés dans le cadre de cette thèse dans un modèle de connectivité régionale. Cet exemple a uniquement vocation à servir de base de discussion sur la pertinence et l'importance de l'inclusion du comportement dans les modèles de connectivité.

In the one which did, behaviour significantly influenced retention

How much could behaviour influence connectivity patterns ?

7.3.2 Exemple de prise en compte du comportement dans un modèle régional

Pour mettre cet exercice dans un contexte opérationnel, nous avons simulé la dispersion larvaire depuis la seule zone protégée côtière de la région (le cantonnement de pêche du Cap Roux ; Figure 4.1) et prédit la dispersion de larves d'une espèce de type Sparidae (une famille ciblée par la pêche traditionnelle côtière). Nous avons étudié l'export depuis ce cantonnement vers les zones adjacentes : quantité de larves exportées, zones d'export, quantité de larves retenues ; autant de paramètres qui contribueraient à l'évaluation de la pertinence de cette zone de protection.

A connectivity model based on our observations

Le modèle et les champs de courants utilisés sont les mêmes que dans le Chapitre 6. Quarante mille œufs sont relâchés entre 0 et 5 m de profondeur dans et autour du cantonnement du Cap Roux, du 7 au 10 juin 2014. Le délai avant éclosion est fixé à deux jours [126]. La durée larvaire est de 16 à 20 jours [232, 241] ce qui place l'arrivée des larves à la côte autour de la nouvelle lune du 27 Juin, comme observée dans le Chapitre 4. Les résultats obtenus avec une simulation considérant les larves comme passives sont comparés à une simulations prenant en compte les différents comportements larvaires décrits ci-dessous.

Après l'éclosion, la migration nyctémérale est simulée selon les distributions verticales observées dans le Chapitre 2. Les larves nagent horizontalement à partir de la flexion (8 jours après l'éclosion [16]). Leur vitesse à la fin de la période larvaire est fixée à 12 cm s^{-1} [Chapitre 6]. Avant, leur vitesse est calculée selon Leis *et al.* [309] (l'accroissement est linéaire). Leur orientation est basée sur un compas solaire [Chapitre 5] et leur permet de suivre une direction cardinale indépendamment de leur position et/ou de leur distance à la côte. Elles nagent donc en s'orientant vers le Nord, ce qui est compatible avec la localisation générale des habitats d'installation dans la région et le fait que les larves de poissons ne sont pas présentes au sud de la zone frontale du courant Liguro-Provençal [Chapitre 2]. La nage en groupe (inférée dans le Chapitre 4) augmente la précision de l'orientation qui est fixée à $k=3,5$, une valeur légèrement supérieure à celle observée chez les individus seuls [Chapitre 5].

Some dispersal patterns are comparable ...

Les deux simulations, passive et active, présentent des points communs (Figure 7.3) : des larves s'installent jusqu'à $\sim 100 \text{ km}$ de leur zone de ponte dans les deux cas et la péninsule de Saint-Tropez, comme la baie de Cannes, sont toujours des zones d'arrivée préférentielle des larves à la côte.

Cependant les différences sont également marquées : +32.5% d'installation totale pour les larves actives, très peu de larves passives sont

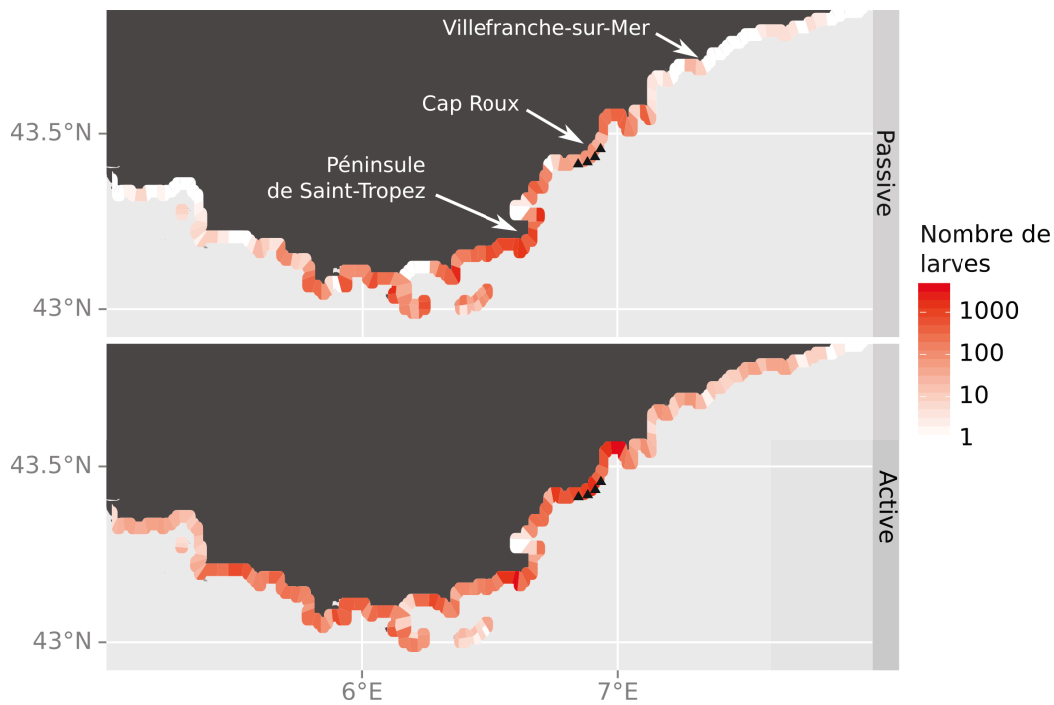


FIGURE 7.3 : Intensité de l'installation à la côte dans les simulations passive (en haut) et avec comportement (en bas). L'échelle de couleur représentant le nombre de larves installées est logarithmique. Les sites de lâcher de particules, situés autour du cantonnement du Cap Roux, sont représentés par des triangles noirs.

retenues à proximité du Cap Roux alors que la majorité des larves actives s'installent à moins de 10 km de celui-ci, le taux de rétention au sein de la zone protégée est de 0,3% pour les larves passives et 3,6% pour les actives ; en même temps un nombre plus élevé de larves actives atteint des habitats distants par rapport aux larves passives, vers l'ouest et le nord-est.

Les conclusions tirées de ces deux simulations quant au rôle du cantonnement de pêche du Cap Roux seraient donc très différentes. L'effet du comportement larvaire pourrait être d'augmenter à la fois le taux de rétention, ce qui favoriserait l'autorecrutement, et la connectivité avec des populations distantes que des larves passives ne peuvent pas atteindre, le tout en combinaison avec la dynamique des courants qui crée les patrons régionaux de dispersion. Ces résultats corroborent les conclusions de Paris *et al.* [346] qui suggèrent que le comportement ne peut donc pas être trivialement considéré comme réduisant simplement les échelles de connectivité, comme cela est souvent fait [13, 340].

... but active larvae settle in much higher numbers ...

... closer to their spawning location

Behaviour increases both retention and long-distance connectivity

Ce travail de modélisation, ainsi que celui du Chapitre 6 mettent également en évidence les manques à combler pour construire des modèles solides et pertinents.

7.3.3 *Vers de meilleurs modèles de connectivité en Méditerranée*

Par essence, les modèles sont plus simples que ne l'est la réalité et sont donc nécessairement imparfaits. Il est nécessaire qu'ils restent simples pour être compréhensibles, mais il ne faut pas qu'ils soient trop simples au point de devenir faux.

The model resolution and the ecological question scales should match

Un critère absolument essentiel est d'utiliser un modèle pour répondre à des questions à des échelles adaptées à la résolution du modèle de circulation et au pas de temps d'intégration utilisés. Dans les deux études de modélisation présentées dans ce travail [Chapitre 6, Section 7.3.2, p. 168], la résolution du modèle utilisé (~1,2 km) ne permettait pas de résoudre les structures de circulation dans la bande côtière. Nous n'avons donc pas cherché à les représenter dans le modèle biologique et considéré que les larves étaient capables de rejoindre la côte lorsqu'elles arrivaient à moins de deux kilomètres de celle-ci (i.e. ~1,5 pas de grille). Toutefois, les patrons prédits par ces modèles ont été interprétés à des échelles de dizaines, voire centaines, de kilomètres, pour lesquelles la résolution de 1,2 km n'est pas limitante. Au contraire, pour répondre à des questions similaires (i.e. la connectivité ou la rétention larvaire régionale), d'autres études se basent sur des résolutions nettement plus basses (e.g. >12 km [340, 347]) ou des pas de temps d'intégration permettant aux larves de traverser plus d'un pas de grille par pas de temps [e.g. 345]. Or, l'utilisation de configurations inadaptées pourraient biaiser les patrons de dispersion obtenus [269]. Pour éviter ces biais et mieux résoudre les phénomènes de circulation à petite échelle, près des côtes, qui sont essentiels pour la dispersion des œufs et, peut-être, l'installation des stades âgés, des modèles hydrodynamiques à plus haute résolution sont essentiels. La configuration d'un modèle régional avec une maille adaptative (plus fine près de la côte, moins fine au large) est en cours d'élaboration [K. Guizien, pers. comm.].

Higher resolution circulation models are needed

Les conditions océanographiques changent en s'éloignant de la côte [Chapitre 2] et varient largement dans le temps [174]. Les patrons de dispersions sont, de ce fait, fortement influencés par les zones et périodes de ponte [348], qui doivent donc être correctement représentés dans les modèles. Or, en Méditerranée Nord-Occidentale, les zones de ponte des Sparidae, par exemple, sont mal connues. Leurs habitats d'installation et de recrutement préférentiel sont, eux, bien documentés mais souvent restreints [233, 349–351]. Par exemple, autour de Marseille (France), l'habitat d'installation des espèces du

Dispersal patterns vary depending on time and location of spawning

genre *Diplodus* serait limité à 9% du trait de côte. L'ensemble de la côte ne devrait donc pas être considéré comme un habitat favorable à l'installation des larves simulées dans les modèles. Cependant, les habitats d'installation ne sont généralement pas explicitement représentés dans les modèles de dispersion car une cartographie précise des habitats, à l'échelle pertinente pour les modèles, n'est pas disponible (e.g. en Méditerranée [Chapitre 6; 340, 345], mais voir Holstein *et al.* [352] pour un exemple en Mer des Caraïbes). Une cartographie des habitats côtiers est actuellement en cours en Mer Ligure [L. Mangialajo, *pers. comm.*, 353] et permettra d'affiner les futurs modèles de connectivité dans la région.

Mapping coastal habitats is necessary to configure spawning and settlement grounds in models

Les simulations présentées dans ce travail insistent sur le fait qu'il est essentiel de prendre en compte le comportement larvaire dans les modèles de connectivité, notamment ceux de migration nycthémerale et de nage orientée qui semblent être les plus importants [Chapitre 6, Section 7.3.2, p. 168; 115, 338]. Le comportement de migration nycthémerale est bien documenté chez les larves de poissons, y compris en Méditerranée [Chapitre 2; 62, 105, 106]. Les larves de Perciformes peuvent nager à des vitesses soutenues [Chapitre 6; 100] et leur morphologie pourrait fournir des indications sur leurs capacités de nage en l'absence de données sur l'espèce d'intérêt [Chapitre 6; 326]. De plus, la vitesse de nage peut également être inférée au cours de l'ontogénie à partir des capacités de nage de larves en phase d'installation, qui sont plus faciles à étudier [16]. Les informations sur les capacités de nage des espèces Méditerranéennes sont rares mais celles sur les capacités d'orientation *in situ* le sont encore plus, et ce partout dans le monde [Section 1.5, p. 34, Chapitre 5]. Or, ce comportement est susceptible d'avoir un impact majeur sur la dispersion, en particulier s'il apparaît dès les plus jeunes stades de développement [275]. Des données supplémentaires à la fin de la phase larvaire, mais aussi et surtout au cours de l'ontogénie, seraient donc actuellement les plus critiques à collecter et à prendre en compte dans les modèles de dispersion. Lorsqu'aucune donnée n'est disponible, le biais associé à leur absence pourrait être estimé en comparant les patrons de dispersion obtenus à partir de simulations passives et d'autres simulant des comportements caricaturaux (nage toujours à haute vitesse et parfaitement orientée) au moins dans le cadre d'une étude de sensibilité (voir [269] pour des suggestions d'implémentation et [345] pour un exemple en Méditerranée).

Data on fish larvae orientation are crucially lacking

Enfin, les deux modèles présentés montrent que le succès de la phase larvaire pélagique est régi à la fois par l'océanographie et par plusieurs comportements, dont les effets peuvent être différents. Cependant, l'effet unitaire de chaque comportement sur la dispersion

Several behaviours = several influences ?

larvaire a rarement été évalué explicitement (mais voir [295, 346] pour des contre-exemples). Il serait donc intéressant de comparer un modèle simulant l'ensemble des comportements larvaires observés avec des versions dégradées, dans lesquels les comportements ont été ôtés un à un, afin de quantifier leur effet respectif et déterminer l'importance de les prendre en compte dans les modèles de connectivité. Cette analyse de sensibilité pourrait guider efficacement la collecte de données empiriques sur le comportement des larves de poissons.

7.4 LES PRINCIPAUX CONCEPTS DE L'ÉCOLOGIE DU RECRUTEMENT SONT-ILS SENSIBLES À LA PRISE EN COMPTE DU COMPORTEMENT LARVAIRE ?

Classic recruitment ecology did not consider larval fish behaviour

Au cours de ce travail, nous avons mis en avant les capacités comportementales des larves de plusieurs espèces de poissons [Chapitres 2, 4, 5, et 6]. Or, aucun des concepts fondateurs de l'écologie larvaire décrits en introduction (Section 1.2, p. 27) ne prend en compte le comportement des larves de poissons.

Tous les comportements larvaires évoqués dans la littérature n'ont pas été observés au cours de ce travail (par exemple, la recherche de nourriture ou la sélection de l'habitat d'installation décrits dans [100]). Cette section s'intéresse en particulier aux comportements que nous avons directement observés ou que nous avons pu inférer à partir de nos observations sur les larves de Perciformes en Mer Méditerranée.

7.4.1 Concepts basés sur la survie des larves pendant la phase pélagique

Most concepts focus on survival ...

L'écologie du recrutement s'est surtout concentrée sur les facteurs déterminant la survie des larves lors de leur phase pélagique. Les concepts de *période critique* [1] et de *match-mismatch* [19, 20] considèrent la productivité et l'abondance globale de proies comme les facteurs essentiels, tandis que les concepts d'*océan stable* [288] et de *fenêtre environnementale optimale* [22] mettent en avant l'importance des processus physiques favorisant ou limitant le nourrissage. D'autres prennent en compte la *durée de stades de vie* [354] ou la *taille*, considérant que les larves ayant une croissance plus rapide et qui seront donc les plus grandes de leur cohorte, seront moins vulnérables que les autres à la mortalité par prédation [23, 24] (cf. Section 1.2, p. 27 pour plus de détails). Enfin, le concept de *loterie* de [28] donne une importance majeure à la mortalité par prédation pendant et après l'installation.

... mediated by feeding success ...

... or predation

Comportements pertinents et influence possible

LES MIGRATIONS VERTICALES NYCTHÉMÉRALES La majorité du zooplancton effectue des migrations nycthémerales et se retrouve concentrée dans les couches de surface la nuit [355]. Ainsi, en suivant les migrations verticales de leurs proies [Chapitre 2], les larves de poissons maximiseraient leur taux de nutrition. De plus, les larves sont plus visibles lorsque l'intensité lumineuse est élevée, c'est-à-dire pendant le jour dans les couches de surface [262]. Se déplacer plus en profondeur le jour, même si ce déplacement semble de faible amplitude en Méditerranée [Chapitre 2], pourrait réduire la détection des larves par les prédateurs visuels, en particulier les poissons juvéniles et adultes. Enfin, ces migrations verticales peuvent s'effectuer à travers la thermocline, ce qui aura une forte influence physiologique sur la vitesse de croissance des larves et donc sur leur survie [55]. Cette influence serait particulièrement marquée en Méditerranée où les différences de températures peuvent être importantes ; par exemple, la température à 20 m de profondeur (la profondeur d'abondance maximale de larves le jour) était de 8°C inférieure à celle de surface en juillet 2013 [Chapitre 2].

Diel vertical migration helps optimising feeding and survival

L'ÉVITEMENT DES PRÉDATEURS À MICRO-ÉCHELLE Nos observations suggèrent que les larves de poissons sont capables d'éviter les zones de plus forte abondance de prédateurs à micro-échelle, au moins pendant le jour [Chapitre 2]. Ce comportement d'évitement pourrait augmenter le taux de survie immédiate des larves de poissons.

Fish larvae may avoid predators at microscale

LE COMPORTEMENT GRÉGAIRE Le comportement grégaire est souvent interprété comme un moyen de protection contre les prédateurs, car ceux-ci sont perturbés visuellement et le risque de prédation est dilué [262, 356]. De plus, se déplacer en groupe améliore les capacités comportementales des larves de poissons [16], notamment pour la détection des proies et des prédateurs [182]. L'existence de comportement grégaire, suggéré au moins à la fin de la phase larvaire chez les larves de poissons [Chapitre 4], pourrait donc diminuer le risque de mortalité par prédation et peut-être augmenter leur efficacité de recherche de nourriture.

Gregarious behaviour may improve detection of prey and predator

LES CAPACITÉS DE NAGE Les larves de poissons capables d'accélérer rapidement ont plus de chances de s'évader en cas de capture par un prédateur que celles peu mobiles [262]. Par ailleurs, se déplacer activement augmente la probabilité de rencontre avec des proies et des prédateurs [182] et il semble que les larves actives ont un taux

Active larvae would have higher escape probability

de survie systématiquement plus élevé que les larves passives [357]. Ainsi, le comportement de nage des larves de poissons pourrait lui aussi augmenter leur taux de survie.

*Settlement timing may
reduce predation*

SÉLECTION DE LA PÉRIODE D'INSTALLATION Le timing précis de l'arrivée des larves à la côte, au jour et même à l'heure près, comme observé dans le Chapitre 4, ne peut être dû qu'au gré des courants et implique certainement des comportements. Le choix du timing d'arrivée peut être interprété comme une solution d'évitement de la prédation. Là encore le comportement augmenterait donc la survie lors d'une phase souvent considérée comme une seconde période critique [30, 358, 359].

Concepts théoriques vs. comportements larvaires

*Larval behaviour may
enhance feeding success
even at low prey
concentration ...*

La prise en compte de ces divers comportements amène à rediscuter les concepts théoriques associés à la survie larvaire. Par exemple, l'importance de la *période critique* (*sensu* Hjort) et le risque de *mismatch* pourraient être plus limités qu'initialement établi ; comme cela a déjà été soulevé plusieurs fois (synthétisé dans [15] et [126]). De même, l'importance des processus physiques de concentration des proies (*océan stable* de Lasker [288] et *fenêtre environnementale optimale* de Cury & Roy [22]) pourrait être contrebalancée par une exploitation efficace de la colonne d'eau par les larves de poissons, ce qui leur permettrait de maintenir des taux de nourrissage plus élevés que lorsqu'elles sont considérées comme passives.

*... and reduce mortality
by predation*

Les taux de prédation et l'importance de ce processus (*Bigger is better* de Anderson [24] et *durée de stade de vie* de Houde [23]) pourraient être surestimés lorsque le chevauchement spatio-temporel entre prédateurs et larves est considéré à grande échelle (e.g. avec des groupes zooplanctoniques gélatineux [62] ou avec des prédateurs nectoniques [360]). En effet, leur capacité à éviter, à micro-échelle, les zones de forte abondance de prédateurs limiterait le risque de rencontre avec des derniers et pourrait mener à surestimer le taux de prédation sur les jeunes larves.

*Prey availability does
not seem to be the
limiting factor in the
region*

Dans notre cas, les processus liés à l'évitement de prédateurs semblent influencer davantage la distribution des larves de poissons que la disponibilité des proies [Chapitre 2]. De même, le comportement des larves en phase d'installation suggère également une stratégie d'évitement de prédateurs [Chapitre 4]. Par ailleurs, nous avons observé un *mismatch* apparent entre zooplancton et larves de poissons [Chapitre 4] et l'année de plus forte installation de larves est aussi celle de *mismatch* le plus fort. Cela soutiendrait l'hypothèse que la disponibilité des proies n'est pas primordiale pour les espèces que

nous avons observées, tandis que l'abondance et la distribution des prédateurs pourraient avoir une importance capitale.

Perspectives de recherche

De nombreuses études se sont intéressées à la distribution du zooplancton et des larves de poissons à plusieurs échelles. La plupart a été conduite à l'aide de filets à plancton et n'apprécie donc pas les processus à micro-échelle (dont l'importance est synthétisée dans la Section 1.3.1, p. 30 et Chapitres 2 et 3). En effet, comme nous venons de le voir, c'est à cette échelle que les comportements larvaires influencent la survie. L'étude de la distribution *in situ* des larves de poissons en relation avec leurs proies et prédateurs à très fine échelle devient accessible grâce au développement de méthodes d'imagerie à haute fréquence et de classification automatique plus performantes, comme celles des Chapitres 2 et 3. Cependant, ces instruments d'imagerie *in situ* ne collectent pas les organismes et ne permettent donc pas l'étude de contenus stomacaux. De plus, l'identification taxonomique ne peut pas être aussi précise qu'avec des filets.

À ce jour, les études sur la recherche de nourriture par les larves et la prédation sur les larves sont principalement basées sur des expériences de laboratoire, en ne considérant qu'une seule proie et/ou prédateur (voir [67, 126] pour des synthèses). Il semble désormais intéressant de combiner des méthodes d'imagerie *in situ* avec l'étude des contenus stomacaux de larves collectées à la plus fine échelle possible (e.g. 5-10 m sur la verticale avec des filets Multinet ou MOCNESS). Cela permettrait de mettre en relation la distribution à micro-échelle des larves de poissons avec celle de leurs proies *réalisées* plutôt que *potentielles* [e.g. Chapitre 2 ; 33].

La simultanéité de l'échantillonnage par imagerie et par filet serait primordiale pour le succès d'une telle étude et cela n'est pas trivial à mettre en œuvre. Seul ISIIS a prouvé son efficacité pour échantillonner des larves de poissons à micro-échelle (cf. [141] et les travaux de Greer *et al.*), notamment car cet instrument échantillonne de plus grands volumes d'eau que les autres méthodes d'imagerie *in situ*. Cependant, il présente deux inconvénients. Le premier est que sa configuration actuelle ne permet pas d'observer les organismes plus petits que 700 μm . Toutefois, un projet est actuellement en cours afin d'ajouter une seconde caméra à plus haute résolution [C. Guigand, *pers. comm.*]. Le second est que sa structure est trop imposante pour être montée sur un filet, par exemple un MOCNESS 1 m² tel que cela a été mis en œuvre avec le VPR [136]. Il serait toutefois envisageable de monter un filet un peu plus petit sur ISIIS, ce qui permettrait d'imager simultanément les larves de poissons, leurs proies et leurs

Imaging techniques and gut contents should be coupled to explore in situ feeding success ...

... along with interactions with competitors and predators

prédateurs et compétiteurs planctoniques à micro-échelle, mais également de collecter des larves pour étudier leurs contenus stomacaux.

Estimating in situ mortality rates due to macropredators will remain tricky

Même avec un tel outil, estimer la mortalité des larves de poissons *in situ*, par la prédation de macroorganismes planctoniques ou nectoniques, resterait inaccessible [67]. Néanmoins, il est intéressant de noter qu'un système de vidéo *in situ* a permis d'observer des comportements d'agrégations chez des larves en phase d'installation [361]. Aussi, une approche alternative aux études de chevauchement spatial entre prédateurs et larves à submesoéchelle serait d'utiliser des instruments vidéo fixes, installés sur des mouillages ou des objets flottants, visant à observer la prédation *in situ*.

Correctement estimer les taux de prédateurs et de nutrition *in situ* est donc un vrai challenge, mais cette étape est indispensable pour pouvoir estimer la survie des larves au cours de leur phase pélagique, que l'on sait primordiale pour estimer le renouvellement des stocks de poissons [346].

7.4.2 Concepts basés sur l'advection par les courants

Other classic concepts focused on advection

Un second groupe de concepts se focalise sur l'influence des conditions océanographiques pour le transport des larves de poissons. Brièvement, le concept de *dérive aberrante* de Hjort [1] suppose que les larves transportées loin des leurs zones d'installation seront systématiquement perdues. En se basant sur ce même principe, le concept de *rétenion stable* de Sinclair [27] prédit que les adultes devront se déplacer pour se reproduire dans des zones permettant la rétenion physique de leur progéniture. Enfin, le concept de *loterie* de Sale [28] considère que le potentiel d'apport de larves sur un site d'installation donné dépend des conditions océanographiques (cf. Section 1.2, p. 27 pour plus de détails).

Comportements pertinents et influence possible

LES CAPACITÉS DE NAGE Les larves de poissons possèdent des capacités de nage non-négligeables, au moins à la fin de la période larvaire [Chapitre 6 ; 100]. Si la nage est *non-orientée*, elle augmenterait la diffusion mais ne modifierait pas, ou peu, l'advection moyenne par les courants.

Swimming towards settlement habitats would increase retention

Cependant, les larves de poissons ont des capacités sensorielles plus développées que les larves des autres organismes marins [123]. Ces capacités sont primordiales pour la détection et la sélection des habitats d'installation à la fin de leur phase pélagique [17]. Par exemple, la nage *orientée* vers les habitats d'installation favoriserait la rétenion [88, 89], y compris chez les larves nageant très lentement [293,

295]. Toutefois, ce comportement n'est possible que suffisamment proche des habitats d'installation pour qu'ils puissent être détectés.

Dans le Chapitre 5, nous avons montré *in situ* l'existence d'un mécanisme d'orientation par rapport au soleil, qui est donc indépendant des signaux côtiers. Cela indique que lorsqu'aucun habitat d'installation n'est détectable, les larves de poissons seraient tout de même capables de nager dans une direction précise. À petite échelle, une larve pondue dans une zone ou masse d'eau non favorable pourrait donc nager directionnellement pour en sortir en utilisant un tel compas cardinal. À plus large échelle, le Chapitre 6 a prouvé que les capacités de nage des larves permettraient à celles ayant dérivé loin d'un habitat d'installation de le rejoindre en seulement quelques jours, avant la fin de leur phase pélagique, en nageant de façon orientée.

Le comportement de nage orientée des larves de poissons leur permettrait donc de largement modifier leur advection par les courants.

LE COMPORTEMENT GRÉGAIRE Le nombre accru de systèmes sensoriels présents dans un groupe d'animaux augmente leur capacité de détection et de réponse à des signaux [362]. Cela a été confirmé chez les larves d'une espèce de poisson, pour lesquelles nager en groupe augmenterait les capacités d'orientation [268] et semblerait également les rendre plus actives (e.g. nage 10% plus rapide quand elles se déplacent en groupes [268]). Ainsi, un comportement grégaire comme celui suggéré par les patrons d'arrivée des larves observés dans le Chapitre 4 permettrait de mieux localiser les habitats d'installation et de focaliser davantage le comportement de nage orientée présentée ci-dessus.

Par ailleurs, la présence de conspécifiques et de prédateurs influencent la sélection de l'habitat d'installation à micro-échelle [17]. Nager en groupe pourrait donc permettre aux larves de poissons d'augmenter leur capacité de détection des habitats les plus favorables, en termes de disponibilité des ressources et de pression de prédation.

LES MIGRATIONS VERTICALES NYCTHÉMÉRALES Les courants sont souvent hétérogènes sur la verticale et des migrations verticales nycthémerales pourraient modifier le transport larvaire. En particulier dans les zones côtières, où les courants sont plus faibles en profondeur, de telles migrations auraient tendance à favoriser la rétention [13, 363]. Cependant, nous avons observé qu'en Mer Ligure les migrations verticales des larves de poissons étaient relativement restreintes par rapport aux variations verticales des courants [Chapitre 2]. Dans la région, le comportement de migration verticale n'aurait donc qu'un effet limité sur l'advection par les courants.

Fish larvae can also orient using coast-independent cues ...

... and significantly modify their drift

Moving in groups may help detecting settlement habitats

Diel vertical migration seems of limited influence in the region

Concepts théoriques vs. comportements larvaires

Nos observations suggèrent que les capacités de nage et d'orientation des larves de poissons leur procurent le potentiel de contrôler leur transport quasi-indépendamment des courants océaniques, au moins à la fin de la phase larvaire pélagique. En particulier, il permettrait à la plupart d'entre elles de rejoindre un habitat d'installation en seulement quelques jours, même en cas de dérive à plusieurs dizaines de kilomètres de la côte. De plus, au vu de la distribution des larves de poissons en Mer Ligure [Chapitre 2] ou ailleurs en Méditerranée Nord-Occidentale [50, 152], une telle dérive semble peu probable. La combinaison entre la rétention physique et la nage orientée pourrait permettre même aux larves les plus lentes d'accéder à un habitat d'installation à la côte. Ainsi, comme le suggère le Chapitre 6, l'étendue des capacités comportementales des larves de poissons nuance l'importance du concept de *dérive aberrante* de Hjort [1]. Cette dérive ne serait finalement aberrante que lorsque les courants sont beaucoup plus rapides que la vitesse de nage des larves ; ce qu'aucune étude ne suggère jusqu'à présent pour les larves de Perciformes [Chapitre 6 ; 289, 290].

Aberrant drift is unlikely to occur in Mediterranean species

Les conditions océanographiques auraient tout de même une influence majeure sur l'advection des stades pélagiques peu mobiles (i.e. œufs et larves pré-flexion). Ces phases peuvent être relativement longues en milieu tempéré froid (jusqu'à plusieurs semaines à <15°C) mais ne dureraient que quelques jours en milieu tropical ou en Méditerranée, puisque la température y est toujours supérieure à 13°C [126]. La pertinence du concept de *rétention stable*, sensu Iles & Sinclair [26] et Sinclair [27], semble confirmée pour les stocks de Hareng de Mer du Nord [364], donc en milieu tempéré froid. Cependant, le développement des capacités comportementales des larves de poissons en milieu chaud montre qu'elles pourraient contribuer activement à leur rétention dès le stade de la flexion [16]. Les similarités entre les larves d'espèces tropicales et de Méditerranée, soulignées aux Chapitres 5 et surtout 6, suggèrent que leurs capacités comportementales réduiraient la nécessité d'une *rétention stable* passive pour le succès de la phase larvaire.

Stable retention has a major importance in cold water species ...

... but seems less relevant for Mediterranean species

Enfin, les capacités comportementales des larves de poissons sont maximales à la fin de la phase pélagique [16, 100] et la sélection du timing et de l'habitat d'installation n'est pas aléatoire [Chapitre 4 ; 17]. Ainsi, l'hypothèse de *loterie* de Sale [28] se verrait en partie modifiée par le fait que le potentiel d'arrivée de larves ne serait en fait pas complètement déterminé par les conditions océanographiques. En effet, le flux de larves serait en partie relié au niveau d'attractivité de l'habitat perçu par les larves de poissons, tandis que la qualité de

Behaviour may also determine the selection of settlement habitats

l'habitat d'installation sélectionné aurait une influence sur le taux de survie post-installation [17].

En conclusion, les différents comportements larvaires que nous avons observés pourraient donc avoir une influence considérable sur l'advection par les courants et, de ce fait, leur prise en compte modifierait profondément les fondements des concepts classiques, en particulier ceux de *dérive aberrante* de Hjort [1] et de *rétention stable* de Sinclair [27].

Perspectives de recherche

Nous avons montré que les larves étaient capables de s'orienter pendant le jour, grâce au soleil. Les études publiées dans la littérature sont en accord avec ce résultat, puisque la plupart ont montré la présence d'une orientation cardinale, qui est fréquemment influencée par des signaux relatifs au soleil [e.g. 116, 124, 273, 274]. Si l'orientation est possible grâce au soleil le jour, la plus grande inconnue devient donc le mécanisme d'orientation la nuit. En effet, la distance à laquelle les habitats côtiers peuvent être détectés grâce au son [117] ou aux odeurs [122] est encore mal définie [119] et il n'existe actuellement aucune preuve d'orientation par rapport au champ magnétique. Les rares études ayant testé les différences de comportement entre le jour et la nuit ont montré que les larves de poissons étaient également actives pendant la nuit [365], voire plus actives que le jour [366] et qu'elles étaient capables de détecter les habitats à proximité ($\ll 1$ km) [278]. Ainsi, il est envisageable que les larves de poissons utilisent le soleil pour s'orienter de façon cardinale pendant le jour, dans une direction qui les rapprocherait des habitats côtiers [124]; une fois entrées dans la zone de détection d'un habitat d'installation côtier, les larves pourraient alors maintenir leur position au large, de jour comme de nuit, en attendant le signal déclenchant leur passage du milieu pélagique vers un habitat d'installation, par exemple la phase de la lune [Chapitre 4]. Par ailleurs, si l'orientation par rapport à une référence céleste est possible (le soleil pendant le jour), il est également possible que les références nocturnes (étoiles, lune, etc.) soient utilisées par les larves de poissons. Il est donc essentiel de déterminer ce que font les larves au large pendant la nuit : sont-elles capables de s'orienter ? Seules des expériences d'orientation *in situ* pourront apporter des éléments de réponses.

S'il est désormais admis que les larves de poissons possèdent des capacités de nage et d'orientation significatives [Chapitres 5 et 6 ; 367], les descriptions de ces capacités sont restreintes à quelques espèces dans quelques environnements (principalement tropicaux). De plus, l'ontogénie du comportement n'a été décrite que chez un encore plus

Fish larvae can orient during the day ...

... but how do they behave at night ?

petit nombre d'espèces [16, 289, 302, 305, 368]. La seule étude comparant le comportement d'orientation entre différentes régions a montré que les larves d'une même espèce avaient une directionnalité comparable (i.e. qu'elles avaient la même capacité à suivre une direction précise), mais qu'elles s'orientaient dans des directions différentes [369]. Les données disponibles ne permettent donc pas de généraliser les comportements observés en un mécanisme d'orientation "universel". De plus, les données ne sont pas toujours disponibles pour les espèces d'intérêt commercial ou sociétal qui motivent les études de connectivité par modélisation (e.g. le mérrou brun pour l'étude de la connectivité entre des aires marines protégées en Méditerranée [340] et les Sparidés pour le Chapitre 6 et la Section 7.3.2, p. 168). Il est donc fondamental de continuer à acquérir des données empiriques *in situ* sur plus d'espèces et dans plus d'environnements.

Orientation cues may be universal, but responses to these cues might not

Further description of in situ orientation is critically needed

Selon le même principe que le concept *bigger is better* [24], il est probable que seules les larves les plus performantes réussissent à survivre et à rejoindre la côte [370]. Bien que la forte variabilité interindividuelle des capacités comportementales soit fréquemment remarquée (y compris dans le Chapitre 6), ses causes restent largement inexpliquées. L'asymétrie a été régulièrement évoquée comme marqueur de la qualité du développement et donc comme proxy potentiel des capacités de nage [e.g. 325]. La condition nutritionnelle des larves semble influencer leur endurance, mais uniquement suite à des périodes de jeûne de plusieurs jours [303]. En plus de décrire les capacités comportementales et sensorielles des larves de poissons, il faudrait donc explorer les causes de la forte variabilité interindividuelle. Une première approche pourrait être de décrire la condition de larves sauvages ayant atteint la côte et de la mettre en relation avec leur capacité de nage [e.g. 303] et d'orientation. Une seconde approche pourrait être de comparer les capacités comportementales de larves sauvages avec celles de larves élevées en laboratoire dans différentes conditions. Ceci permettrait de déterminer si les larves de poissons ayant survécu à la phase larvaire pélagique sont effectivement les plus performantes.

Inter-individual variability is high and causes are unknown

Which cues are actually relevant, when, and at which scales?

Par ailleurs, il est également admis que la sélection des sites d'installation n'est ni aléatoire, ni passive [17], mais les échelles spatiales auxquelles se jouent leur détection et leur sélection ne sont pas résolues. Une meilleure compréhension de l'utilisation des signaux relatifs ou indépendants de la côte, à différentes distances de celle-ci et pour plusieurs stades ontogéniques, permettrait d'améliorer les modèles de dispersion, en particulier en rendant plus réaliste la phase d'installation. Il en est de même pour le comportement d'agrégation pré-installation, dont nous ne savons que peu de choses si ce n'est

qu'il est potentiellement très répandu [Chapitre 4]. Il serait donc utile d'estimer l'influence de la nage en groupe sur la détection et la sélectivité du choix de l'habitat d'installation.

CONCLUSION GÉNÉRALE

Dans son travail fondateur au début du 20^{ème} siècle, [Hjort](#) a mis en avant une possible importance de la rétention larvaire pour le renouvellement des stocks de poissons. Par ailleurs, l'autorecrutement est essentiel pour le maintien de populations isolées et il est plus facile à estimer que la dispersion larvaire [72]. Cela explique probablement la multitude d'études focalisées sur la rétention larvaire, cherchant directement ou indirectement à estimer les taux d'autorecrutement [82, 91, 371]. Ces approches donnent un poids majeur aux processus hydrographiques ou comportementaux permettant la rétention des larves à proximité de leur zone de ponte.

Pour permettre la rétention, les larves d'espèces côtières devraient profiter de conditions hydrographiques particulières (tourbillons stables par exemple) et/ou être capables de détecter, à distance, ces zones favorables et s'y maintenir pendant toute la phase pélagique. Les mécanismes évoqués pour cela sont une migration verticale [93] ou une nage orientée [275, 365] précoces. À ce stade, la nage aurait un coût énergétique très élevé [372], nécessitant donc que les proies des larves soient abondantes dans les zones de rétention. Comme il est peu probable que ces conditions soient toujours réunies, cette stratégie de rétention pourrait donc être associée à une croissance potentiellement lente due au coût de la nage. À l'inverse, une stratégie non focalisée sur la rétention permettrait une croissance plus rapide, puisque moins d'énergie serait dépensée pour se maintenir près de la côte et pourrait donc être allouée à la croissance. Par ailleurs, une dispersion plus étendue dans le cadre de cette stratégie permettrait à certains individus au moins d'accéder à des zones de nourrissage potentiellement plus favorables que les zones de rétention.

L'ensemble des résultats obtenus au cours de ce travail, en particulier la dispersion vers des zones où les courants sont plus forts [Chapitre 2], l'existence d'un comportement d'évitement de prédateurs à microéchelle [Chapitre 2], d'un mécanisme d'orientation précis indépendant des habitats côtiers [Chapitre 5] et de capacités de nage élevées à la fin de la période larvaire [Chapitre 6], quand leur coût énergétique serait moindre [372], suggèrent que les larves que nous avons testées seraient adaptées pour exploiter efficacement le milieu pélagique et rejoindre la côte activement au moment de l'installation plutôt que pour favoriser la rétention. Cela suggère que ces larves suivraient principalement la seconde stratégie, avec une croissance plus rapide et une dispersion plus élevée.

Une seconde période critique est régulièrement suggérée entre la phase d'installation et le recrutement [30, 358, 359]. De plus, les larves en meilleure condition à l'issue de leur phase larvaire ont plus de chances d'y survivre [370]. Cette stratégie privilégiant la croissance et la qualité de l'habitat larvaire plutôt que la rétention à proximité des zones de pontes pourrait se montrer favorable même après l'installation.

Cela soulève la question, plus large, de la dispersion comme raison évolutive de la phase larvaire. La phase larvaire est-elle pélagique car la dispersion est capitale au maintien des populations ou car l'habitat de l'océan ouvert est plus favorable pour les jeunes stades de développement ? Cette thèse montre que les capacités des larves de poissons à éviter les prédateurs, se mouvoir, s'orienter, etc. influencent les compromis et les hypothèses habituellement considérés lors de la phase larvaire des organismes marins côtiers. Une meilleure connaissance des capacités comportementales des larves de poissons est donc nécessaire pour décrire la connectivité entre les populations mais pourrait également éclairer des questions plus larges, notamment sur son origine évolutive.

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ABSTRACT

Most coastal fish species have a bipartite life history, with a demersal phase as juvenile and adult and a pelagic larval phase. Dispersal is often limited to this pelagic phase, which is also the phase experiencing the highest mortality rates. Predicting the connectivity between populations remains difficult because not all processes determining larval fish survival and transport during the pelagic phase are understood. Besides the environmental conditions that may influence the journey of fish larvae in the open ocean, these tiny organisms possess high behavioural abilities (swimming, orientating, etc.) that have the potential to shape their dispersal. However, the vast majority of *in situ* observations of these behaviours have been conducted in tropical environments and very little data exists on temperate Perciformes fish larvae. In this dissertation, we aim to describe the ecology and behavioural abilities of fish larvae from the Mediterranean Sea, a temperate environment where they have never been studied.

The first part of this dissertation describes the distribution of young fish larvae along an inshore-offshore transect crossing a hydrological front. We also describe their diel vertical migration and predator-avoidance behaviour. The high-frequency imaging techniques used to capture their distribution at microscale generated huge amount of data. It lead us to modify an automatic classification method to reduce the time required to processes these kind of data. The second part focuses on the settlement phase, when fish larvae come back to the coast at the end of their pelagic journey. To shed light on the factors influencing the settlement process, we monitored the supply of fish larvae to a coastal habitat, on a weekly basis for three years and at higher frequency over shorter periods of time. Additionally, we tested the *in situ* orientation abilities of the most abundant species, focusing on large scale orientation mechanisms. In the laboratory, we measured the swimming speeds of several species, including the ones tested for orientation. Then, we implemented these observed behaviours in a biophysical model to explore their combined influence on settlement rate. To finish, we discuss on how larval fish behaviour may influence survival throughout the pelagic larval phase and insist on the importance of considering behaviour to improve larval dispersal models.

RÉSUMÉ

La majorité des espèces de poissons côtiers a un cycle de vie comprenant une phase juvénile et adulte démersale et une phase larvaire pélagique. Cette seconde phase représente l'unique opportunité de dispersion pour de nombreuses espèces mais est soumise à une forte mortalité. Aujourd'hui, il est toujours délicat de prédire la connectivité entre les populations car tous les processus influençant la survie et le transport des larves durant leur phase pélagique ne sont pas encore décrits. Les larves de poissons possèdent des capacités comportementales non-négligeables (de nage, d'orientation, etc.) qui pourraient leur permettre de contrôler leur dispersion au cours de leur épisode pélagique. Cependant, les observations *in situ* de ces comportements ont principalement été faites en milieu tropical. Elles sont nettement plus rares en milieu tempéré, notamment chez les poissons Perciformes. Dans cette thèse, nous cherchons à décrire l'écologie et les capacités comportementales des larves de poissons en Mer Méditerranée Nord-Occidentale, un milieu tempéré où elles n'ont pas encore été décrites.

La première partie de cette thèse vise à décrire la distribution des jeunes stades larvaires le long d'un transect côte-large traversant un front hydrologique. Nous nous intéressons également à leurs comportements de migration nyctémérale et d'évitement des prédateurs. La méthode d'imagerie utilisée pour décrire leur distribution à micro-échelle générant des quantités de données considérables, nous avons développé une méthode de classification automatique pour accélérer le traitement de ce type de données. La seconde partie se concentre sur la phase d'installation, c'est-à-dire lorsque les larves arrivent à la côte à la fin de leur phase pélagique. Nous avons suivi l'arrivée des larves à la côte afin de déterminer les périodes d'installation des différentes espèces ainsi que les facteurs influençant leur arrivée. Nous avons également testé *in situ* les capacités d'orientation des espèces les plus abondantes, en se focalisant sur les mécanismes d'orientation à large échelle. En laboratoire, nous avons mesuré les vitesses de nage de plusieurs espèces, incluant celles testées pour l'orientation. Nous avons ensuite implémenté ces comportements observés dans un modèle biophysique afin de tester leur influence combinée sur le taux d'installation. Pour finir, nous discutons de l'influence que peut avoir le comportement sur la survie des larves de poissons tout au long de la phase pélagique, ainsi que de l'importance de sa prise en compte dans les modèles de dispersion.