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**Relation entre le régime alimentaire et la morphologie durant le développement larvaire chez différentes espèces de poissons du golfe du Saint-Laurent**

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PAR

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*A Toute ma famille*

*A ma chère maman Nazihā*

*A l'amour de ma vie Khalifa Ben Arabia*

*A ma très chère tante Khadouja*

*A mes deux frères Hoyssem et Aymen*

*A tous ceux que j'aime et qui m'aiment,*

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 ... **SARRA**



## **AVANT-PROPOS**

Ce mémoire de maîtrise est composé de trois chapitres : les premier et dernier chapitres correspondent respectivement à l'introduction générale et la conclusion générale rédigées en français, alors que le deuxième chapitre est présenté sous forme d'article scientifique rédigé en anglais. Cet article est le fruit d'une collaboration de trois auteurs, dont moi-même qui est le premier auteur. J'ai dirigé et contribué aux analyses en laboratoire, réalisé les différentes analyses statistiques, l'interprétation des résultats ainsi que la rédaction du mémoire.

Les échantillons de 11 espèces de larves de poissons utilisés dans le cadre de cette étude proviennent des collections récoltées lors des campagnes d'échantillonnage du réseau GLOBEC-Canada (1997-2000) effectuées par l'équipe du professeur Louis Fortier.



## RÉSUMÉ

Les fluctuations dans l'abondance des populations de poissons sont en grande partie régulées par le taux de survie lors du stade larvaire. La survie des larves dépend fortement du succès d'alimentation qui dépend à son tour du chevauchement spatio-temporel entre l'émergence des larves de poissons et la production de leurs proies planctoniques préférées. Ce couplage étroit entre l'alimentation des larves et leur survie souligne la nécessité d'identifier les facteurs potentiels qui déterminent les préférences alimentaires d'un stade critique du cycle de vie des poissons. La présente étude a été conçue pour étudier l'influence potentielle des caractéristiques morphologiques sur la sélectivité alimentaire des larves. Nous avons comparé le régime alimentaire de 11 espèces de larves de poissons de morphologie variable (partagées en 4 ordres et 8 familles) capturées au même moment dans le plancton et s'alimentant donc de proies présentes dans le même assemblage zooplanctonique. Afin de procéder à une comparaison formelle de la niche alimentaire, le contenu stomacal d'un total de 247 larves a été analysé et les proies ingérées ont été identifiées au niveau taxonomique le plus fin possible. La sélectivité des larves pour leurs proies a été déterminée en comparant l'abondance relative des proies retrouvées dans les estomacs à celle dans l'environnement. Malgré la grande diversité morphologique qui existe entre les espèces de larves, la forte majorité des espèces ont sélectionné, indépendamment de leur taille, les stades nauplii du copépode calanoïde *Pseudocalanus* sp.. Par conséquent, le comportement des larves et de leurs proies potentielles est probablement plus important pour influencer la composition du régime alimentaire que les caractéristiques morphologiques des prédateurs. Nos résultats suggèrent également que la variabilité dans l'abondance et la phénologie de cette proie clé (*Pseudocalanus* sp.) a le potentiel de moduler la force du recrutement de nombreuses espèces de poissons du golfe du Saint-Laurent.

**Mots clés :** Larves de poissons, morphologie, sélectivité alimentaire, *Pseudocalanus* sp.



## ABSTRACT

Fluctuations in the abundance of fish populations are largely regulated by survival during the larval stage. Larval survival is highly dependent on feeding success, which in turn depends on the spatio-temporal overlap between the emergence of larval fish and the production of their preferred planktonic prey. This tight coupling between larval feeding and survival underscores the need to identify potential factors that determine the feeding preferences during a critical stage of the fish life cycle. The purpose of the present study was to investigate the potential influence of morphological characteristics on larval feeding selectivity. We compared the diets of 11 species of larval fish of different morphology (4 orders and 8 families) captured at the same time in the plankton and thus feeding on prey present in the same zooplankton assemblage. To compare the feeding niches, stomach contents of a total of 247 larvae were analyzed and ingested prey were identified to the lowest taxonomic level possible. Prey selectivity was determined by comparing the relative abundance of prey found in the stomachs to that in the environment. Despite the great morphological diversity among larval species, the strong majority of species selected, regardless of their size, the naupliar stages of the calanoid copepod *Pseudocalanus* sp.. Hence, the behavior of larvae and their potential prey is likely more important in influencing diet composition than morphological characteristics of the predators. Our results also suggest that variability in the abundance and phenology of this key prey (*Pseudocalanus* sp.) has the potential to modulate the strength of recruitment of several Gulf of St. Lawrence fish species.

**Keywords:** Larval fish, morphology, prey selectivity, *Pseudocalanus* sp.

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# CHAPITRE 1 :

## INTRODUCTION GÉNÉRALE

### 1.1 Alimentation larvaire : croissance, survie et recrutement

La phase larvaire a une importance cruciale en termes démographiques pour les populations de poissons. Depuis les travaux de Hjort (1914, 1926), on admet généralement que le recrutement d'une population de poissons est en grande partie lié à la survie au stade larvaire (Houde 1987; Anderson, 1988; Cushing, 1990; Leggett & Deblois, 1994; Houde, 2008). On associe cette relation au taux de mortalité extrêmement élevé qui caractérise la période de transition de l'alimentation endogène basée sur les réserves vitellines à une alimentation exogène basée sur la consommation de proies planctoniques (Anderson, 1988; Hjort, 1926; Castonguay *et al.*, 2008; Houde, 2008; Leggett & Frank, 2008). Cette période est généralement connue comme une période critique pour la survie des larves de poissons (Hjort, 1914) pendant laquelle la nouvelle cohorte est réduite à un nombre relativement faible de larves survivantes qui contribueront au recrutement subséquent au sein de la population (Govoni, 2005). La variabilité interannuelle du recrutement est élevée et fortement liée aux variations du taux de mortalité pendant la transition alimentaire (e.g. Shepherd & Cushing 1980; Peterman *et al.*, 1988; Platt *et al.*, 2003). Le concept de la "période critique" de Hjort (1914 ; 1926) a été complété par des hypothèses plus spécifiques qui expliquent comment la variabilité dans la disponibilité de la nourriture peut être liée au succès du recrutement. La première est l'hypothèse "bigger is better" qui propose que les larves de grande taille sont moins vulnérables à la prédation que les larves à petite taille du même âge (Miller *et al.*, 1988). Cette hypothèse est étroitement liée au deuxième concept "stage-duration" qui se concentre sur le temps passé dans les classes de taille plus petites et vulnérables. Ce concept

suggère que les larves à croissance rapide se métamorphosent au stade juvénile à un âge inférieur à leurs conspécifiques à croissance lente, ce qui diminue la durée du stade larvaire et augmente par la suite le taux de survie (Chambers & Leggett, 1987). Une troisième perspective est l'hypothèse "growth-selective predation", basée sur des observations selon lesquelles à une même taille, les larves à croissance lente sont plus susceptibles à la prédation, puisqu'elles sont en moins bonne condition physiologique (Takasuka *et al.*, 2003).

La croissance et la survie des larves dépendent largement de la réussite de la première nutrition, qui dépend à son tour de la disponibilité de proies adéquates en quantité suffisante au cours des premiers stades d'alimentation (Hjort, 1914; Lasker, 1975; Cushing, 1990; Bakun, 1996; Houde, 2008). En général, l'éclosion larvaire de plusieurs espèces est synchronisée avec la production accrue des proies planctoniques (Cushing, 1990). La coïncidence spatiale (Triade de Bakun [1996]) et temporelle (hypothèse du « match-mismatch » de Cushing [1990]) entre l'émergence des larves et la production de leurs proies préférées déterminerait le succès de la nutrition larvaire, ainsi que la probabilité de survie. Le nombre de larves survivantes pendant le stade larvaire constitue un indice fiable de la force de la classe d'âge (Leggett & Deblois, 1994; Platt *et al.*, 2003). Un fort chevauchement spatio-temporel entre le bloom planctonique et le pic de production larvaire d'une espèce donnée se reflète par de fortes classes d'âge grâce à une alimentation optimale et une croissance rapide des larves. Au contraire, un chevauchement faible ou nul aboutit à un taux de survie extrêmement faibles et donc un recrutement infructueux en raison d'une croissance lente et d'une mortalité en masse par famine. Des études ont révélé que le taux de croissance des larves est intimement lié à leur efficacité de recherche et de capture des proies, et ont constaté qu'une croissance rapide est souvent associée à des taux d'alimentation élevés (Østergaard *et al.*, 2005; Dower *et al.*, 2009; Robert *et al.*, 2014). Pepin *et al.* (2015) ont trouvé qu'en moyenne, les individus avec une plus grande quantité de proies dans leur estomac avaient des taux de croissance plus élevés.



En raison du développement limité des systèmes d'alimentation et sensoriels nécessaires pour localiser, capturer et transformer les proies (Poling & Fuiman, 1998, 1999; Anto *et al.*, 2009; Anto & Turingan, 2010), les poissons sont plus sensibles à la famine au début de leur cycle biologique que les poissons juvéniles ou adultes (Nunn *et al.* 2012). De plus, le stade larvaire est caractérisé par une faible résistance à la famine allant de quelques heures à quelques jours selon l'espèce (Houde, 2002; May, 1974). Des études (Ehrlich *et al.*, 1976; Miller *et al.*, 1988) ont montré que la résistance à la famine augmente avec l'âge et la longueur des larves. Toutefois, après l'atteinte d'un point de non-retour (PNR) lors d'une période de jeûne prolongée, la larve affaiblie devient incapable de se nourrir efficacement de la ressource disponible. Elle épuise alors ses réserves énergétiques et finit par mourir même en présence de nourriture (May, 1974; Gatesoupe *et al.*, 1999; Houde, 2002). Le PNR est souvent utilisé comme un indice pour évaluer la tolérance des larves de poissons à la famine (Yokota *et al.*, 2016) et pour comprendre la relation entre la capacité de première alimentation des larves et leur taux de survie (Shan *et al.*, 2008). En plus de la mortalité directe par famine, les larves affamées qui deviennent affaiblies sont sensibles à d'autres sources de mortalité telles que la prédation (Drolet *et al.*, 1991; Green & McCormick, 2001). Une période de famine relativement courte peut également entraîner des malformations et/ou des problèmes permanents d'alimentation et de digestion chez les larves survivant au-delà du PNR (Dou *et al.*, 2002). En général, la mortalité pendant le stade larvaire est considérée comme un mécanisme clé entraînant des fluctuations dans le recrutement des stocks de poissons (Houde, 1989).

## **1.2 Les facteurs contrôlant la sélectivité alimentaire des larves de poissons**

### **1.2.1 Les facteurs environnementaux**

Des études sur la variabilité du recrutement mettent aujourd'hui l'emphase sur les facteurs qui contrôlent la sélectivité alimentaire d'un stade critique du cycle de vie des poissons. La sélectivité alimentaire des larves peut varier selon les conditions environnementales physiques (température et la turbidité de l'eau (matières en suspension, etc.) et trophiques (tels que la disponibilité de proies, leur abondance et/ou densité, la compétition et la prédation) du milieu. Les larves de poissons sont des organismes planctoniques dotés d'une faible capacité natatoire ne leur permettant pas de se déplacer à contre-courant. Dans certains cas, les courants marins peuvent éloigner les larves de poissons de leur zone d'alimentation, ou disperser spatialement les organismes du zooplancton, ce qui diminue les chances de rencontres entre les larves et leurs proies potentielles, et affecte par la suite les schémas de sélectivité alimentaire (Iles & Sinclair, 1982; Fortier *et al.*, 1992). De plus, les forces exercées par la viscosité du milieu peuvent limiter la capacité des larves à capturer des proies de petites tailles lors du stade de la première alimentation. China & Holzman, (2014) ont attribué la famine lors de la première alimentation aux considérations hydrodynamiques du milieu dans lequel de faibles nombres de Reynolds, et donc une forte viscosité, limitent mécaniquement le succès alimentaire des larves, même en présence de densités de proies élevées. La turbulence est l'un des autres facteurs hydrodynamiques susceptibles d'exercer des effets considérables sur la sélection des proies des larves de poissons. Sur la base des travaux de Rothschild & Osborn (1988), qui indiquent que la turbulence augmente le taux de contact entre les espèces planctoniques, on peut déduire que le taux de rencontre entre les larves de poissons et leurs proies potentielles augmente dans un milieu à écoulement turbulent caractérisé par des fluctuations aléatoires des gradients. Dans certains cas, les larves sont capables d'effectuer des mouvements limités pour faire face aux facteurs environnements susceptibles d'affecter leur sélectivité alimentaire et leur survie. Ces déplacements consistent en des migrations verticales leur permettant d'accéder à des courants plus favorables (Grioche *et al.*, 2000) ou bien à des zones de turbulence limitée afin d'éviter les vitesses d'écoulement trop élevées (Fortier & Leggett, 1983).

La sélectivité alimentaire des larves de poissons dépend non seulement des conditions environnementales du milieu marin, mais aussi de la composition de l'assemblage zooplanctonique. En fonction de la richesse du milieu en proies, les larves de poissons adoptent de nouvelles stratégies de recherche de nourriture et de grands changements peuvent être observés dans leur comportement alimentaire. Par exemple, afin de compenser le manque de proies lors de mauvaises conditions d'alimentation, certaines espèces de poissons peuvent être obligées d'augmenter la largeur de leur niche trophique pour minimiser le temps passé à chercher des proies et ainsi gagner de l'énergie par effort de capture de proies (Werner & Hall, 1974). Une étude réalisée par Munk (1995) sur le comportement alimentaire de la morue *Gadus morhua* a révélé une augmentation de l'activité de nage des larves à la suite de la diminution de la densité des proies. Cependant, une augmentation de la densité des proies est susceptible d'augmenter le taux d'ingestion des larves jusqu'à saturation (Ellertsen *et al.*, 1989; Robert *et al.*, 2009). À l'échelle individuelle, la densité des proies potentielles dans le milieu affecte fortement les rencontres stochastiques prédateurs-proies, qui sont elles-mêmes liés à la perception et à la vitesse de nage des larves. En théorie, les larves plus âgées et donc plus grandes sont mieux adaptées pour se nourrir efficacement de la ressource disponible car elles peuvent voir les taxons de proies mobiles à de plus grandes distances que les jeunes larves qui ont une capacité limitée à détecter, capturer, ingérer et digérer les proies potentielles (Sabatés & Saiz, 2000). Au fur et à mesure que les larves grandissent, la taille de la bouche augmente, les performances de nage et la vitesse soutenue et en rafale se renforcent, l'acuité visuelle se développe, la distance de perception et la capacité de recherche et d'ingestion s'améliorent. Ces changements ontogénétiques entraînent souvent des modifications de la composition du régime alimentaire (Nunn *et al.*, 2012; Peck *et al.*, 2012).

### 1.2.2 Rôle des facteurs morphologiques dans l'alimentation des larves de poissons

Le stade larvaire correspond à la poursuite des processus ontogéniques entamés au stade embryonnaire et le début d'une période de transformations physiologiques, anatomiques et morphologiques importantes, accompagnée d'un accroissement de la masse corporelle en réponse à l'alimentation externe (Gatesoupe *et al.*, 1999). Tout au long du cycle biologique pré-métamorphique des poissons marins, la morphologie de la larve est considérée comme un facteur de première importance dans le processus de recherche et de capture de proies (Østergaard *et al.*, 2005). Suite aux changements morphologiques que subit l'individu au cours du stade larvaire, les habitudes alimentaires peuvent changer. Sabaté & Saiz (2000) ont démontré que la sélection des proies change tout au long du développement larvaire et qu'elle varie d'une espèce à l'autre et même entre les groupes de taille d'une même espèce. Selon ces auteurs, la variabilité dans les préférences alimentaires individuelles est dans une certaine mesure associée à des différences morphologiques interspécifiques. Selon Østergaard *et al.* (2005), ces différences alimentaires sont susceptibles de réduire la concurrence inter- et intra-spécifique pour la ressource alimentaire.

Les différences interspécifiques dans le développement de la bouche interviennent fortement dans le succès de la survie des larves de poissons puisqu'elles constituent un déterminant majeur de la variation des types et des tailles de proies consommées (Keast & Webb, 1966; Hunter, 1981). Il a été démontré que les variations dans la taille de la bouche sont proportionnelles à celles de la longueur de la larve (Walford & Lam, 1993; Kamali *et al.*, 2006). L'étude de Sabaté & Saiz, (2000) a révélé que la morphologie de *Notolepis rissoi*, caractérisée par un corps allongé et une bouche de taille relativement petite, peut limiter la taille de ses proies. Pepin (2022) a proposé que la relation entre la taille du corps et de la bouche, et la variabilité qui existe dans la relation, soient considérées comme base pour évaluer les différences de succès alimentaire entre les espèces ainsi qu'entre les individus au sein d'une même cohorte et entre les cohortes.

La capture de nourriture est favorisée par le développement précoce d'autres caractéristiques morphologiques spécifiques comme par exemple l'apparition des dents (Conway *et al.*, 1999). En ce qui concerne la profondeur du corps, il a été démontré qu'elle ne définit pas des limites de la taille des proies ingérées, mais elle affecte le comportement de chasse des larves et donc leurs préférences alimentaires par une influence sur la capacité et la vitesse de nage et de manœuvre (Østergaard *et al.*, 2005). Il existe une grande variété de formes du tube digestif entre les espèces de larves de poissons. Des études ont suggéré que la morphologie et la capacité intestinale déterminent en grande partie la taille des proies et le taux d'ingestion, et déterminent partiellement les choix alimentaires tels que le passage à la piscivorie (Govoni *et al.*, 1986; Ronnestad *et al.*, 2013).

La sélection de certains types et/ou tailles de taxons par rapport à d'autres indique que les caractéristiques morphologiques propres à chaque taxon sont également importantes dans le processus de sélection des proies (Nunn *et al.*, 2012). Ghan & Sprules (1993), par exemple, ont constaté que les jeunes larves de lotte (*Lota lota*, Gadidae) préféraient le rotifère globulaire *Asplanchna* sp. par rapport aux rotifères à épines, ce qui suggère que les rotifères à épines peuvent augmenter le temps de manipulation des poissons qui tentent de s'en emparer. En effet, à la suite d'une augmentation de la taille, les proies améliorent leurs performances de nage et de mobilité (Folkvord & Hunter, 1986; Blaxter & Fuiman, 1990) et leurs mécanismes de défense deviennent plus robustes (par exemple la présence des épines) (Scharf *et al.*, 2000).

### **1.3 Le golfe du Saint-Laurent**

Le golfe du Saint-Laurent (GSL) constitue une vaste mer semi-fermée reliant le fleuve Saint-Laurent à l'océan Atlantique par les détroits de Belle-Isle au nord-est et de Cabot au sud-est. Selon les processus bathymétriques et océanographiques, le ministère des Pêches et des

Océans (MPO) divise cette mer semi-fermée en deux grandes régions : la partie nord du GSL (NGSL ; divisions 4R, 4S de l'Organisation des pêches de l'Atlantique Nord-Ouest [OPANO]) et la partie sud du GSL (SGSL ; division 4T de l'OPANO). Ces deux régions diffèrent par la profondeur de l'eau (Dutil *et al.*, 2011), la composition des communautés biologiques (Plourde & McQuinn, 2010), la diversité et la production ichtyoplanctonique (de Lafontaine *et al.*, 1991; White & Johns, 1997). Toutefois, dans l'ensemble du GSL, les concentrations élevées des nutriments provenant du mélange hivernal créent dans la couche de surface les conditions favorables pour une prolifération phytoplanctonique intense (Le Fouest *et al.*, 2010). Celle-ci est rapidement suivie d'une reproduction estivale des espèces zooplanctoniques, principalement des copépodes qui peuvent représenter jusqu'à 88% du zooplancton (de Lafontaine *et al.*, 1991). Cette période hautement productive coïncide avec l'émergence de nombreuses espèces de larves de poissons qui utilisent ces espèces à tous les stades de développement comme principale source de nourriture. Ces caractéristiques font du GSL une importante zone de pêche commerciale.

Au début des années 1990s jusqu'à la fin du XXe siècle, le GSL a connu une chute drastique des stocks de poissons de fond. L'effondrement a fortement touché la morue de l'Atlantique (*Gadus morhua*), une espèce largement répandue dans l'océan Atlantique Nord, et d'autres stocks comme par exemple, le sébaste (*Sebastes* spp.), la plie canadienne (*Hippoglossoides platessoides*) et la limande à queue jaune (*Limanda ferruginea*). Les principaux poissons-proies de ces prédateurs supérieurs sont le capelan (*Mallotus villosus*), le lançon (*Ammodytes* spp.), le maquereau bleu (*Scomber scombrus*), la stichée arctique (*Stichaeus punctatus*) et la lompénie-serpent (*Lumpenus lampretaeformis*) (Lilly & Fleming, 1981; Scott & Scott, 1988; Morissette *et al.*, 2003; Savenkoff *et al.*, 2004). Conformément à la théorie du forçage descendant et suite au relâchement de la pression de prédation, l'abondance moyenne de plusieurs larves d'espèces fourrages, principalement la stichée arctique (*Stichaeus punctatus*) et la lompénie-serpent (*Lumpenus lampretaeformis*), a augmenté (Bui *et al.*, 2010). Cependant, la même étude a démontré que l'abondance des

larves de lançons *Ammodytes* spp. du nord-ouest du GSL n'ont pas été affectées par la forte réduction des principaux prédateurs et leur abondance est restée stable.

Le rapport de Blais *et al.* (2021) montre une baisse récente de la biomasse zooplanctonique dans le SGSL. Cette baisse de biomasse serait généralement associée à une diminution de l'abondance des espèces de zooplancton de grande taille comme par exemple le grand copépode calanoïde *Calanus hyperboreus*, une espèce subarctique originaire de la mer du Labrador qui a envahi le GSL par l'intrusion sporadique de masse d'eau à travers le détroit de Belle-Isle (Petrie *et al.*, 1988; Koutitonski, 1989; Smith *et al.*, 2006). Face à cette diminution d'abondance des grands calanoïdes, la communauté zooplanctonique a connu une augmentation de l'abondance de petit calanoïde *Pseudocalanus* spp. dans toutes les sous-régions du GSL en 2019, surtout pendant l'automne (Blais *et al.*, 2021). Une nouvelle communauté dominée par une combinaison de petits calanoïdes et de non-copépodes, principalement des larves d'organismes benthiques, s'est installée. Ce changement récent pourrait avoir des implications relativement à l'alimentation des larves de poissons et du recrutement des stocks de la région.

## 1.4 Objectifs

La présente étude vise à améliorer nos connaissances sur l'importance des caractéristiques morphologiques pour déterminer le régime alimentaire et le succès d'alimentation de 11 espèces de larves de poissons (partagées en 4 ordres et 8 familles) capturées en même temps et s'alimentant donc sur le même assemblage zooplanctonique, à travers quatre sous-objectifs :

- (i) Caractériser la communauté zooplanctonique des stations étudiées ;
- (ii) Décrire et comparer le régime alimentaire des espèces larvaires ;

- (iii) Évaluer la sélectivité alimentaire entre les espèces sur la base des ressources alimentaires disponibles dans le champ de proies au moment de la capture ;
- (iv) Comparer les niches alimentaires pour déterminer les possibilités d'interactions alimentaires entre des espèces de poissons de morphologie différente.



**CHAPITRE 2:**  
**THE RELATIONSHIP BETWEEN DIET AND MORPHOLOGY**  
**DURING LARVAL DEVELOPMENT IN DIFFERENT FISH**  
**SPECIES OF THE GULF OF ST. LAWRENCE**

**2.1 INTRODUCTION**

Understanding the causes of fluctuations in fisheries resource abundance has been one of the great challenges of fisheries science for more than a century (Houde, 2008). Since the work of Hjort (1914), which was a prelude to several other studies on larval ecology, it is generally accepted that fluctuations in the abundance of fish populations are largely regulated by the survival rate during the larval stage, and in particular during the period of transition to an exogenous diet based on the consumption of planktonic prey after the depletion of vitelline reserves (Hjort, 1926; Houde, 2008; Leggett & Frank, 2008). This period is generally known as a critical period for larval fish survival (*sensu* Hjort, 1914) during which the new cohort is reduced to a small number of surviving larvae that will contribute to subsequent recruitment (Govoni, 2005). Higher than average mortality during the critical period results in relatively low survival of the cohort and subsequent year-class strength (Leggett & Deblois, 1994; Platt *et al.*, 2003). In this context, variability in survival during the first days of feeding would drive interannual differences observed in the abundances of adult fish, and has the potential to modulate population dynamics.

Many factors determine the survival and growth of fish larva. Hjort's (1914) concept argues that the survival of fish larvae, and therefore year-class strength, is highly dependent on feeding success during the early life stages of the fish. This hypothesis has been further developed by several researchers. It has been shown that larval feeding success is determined by the spatial (e.g. Bakun's triad, 1996) and temporal (e.g. Cushing's match-mismatch

hypothesis, 1990) coincidence between larval emergence and peak production of their preferred prey. This close coupling between larval feeding and survival underscores the need to understand the factors that affect larval preference for certain types and sizes of ingested prey. Prey ingestion is the result of a process influenced not only by environmental variables, but also by several other rarely studied parameters which could be responsible for limiting the number and/or size of ingested prey. Despite decades of research on the feeding ecology of larval fish, very few studies asked how prey selection patterns can be influenced by individual larval morphological characteristics (e.g. Last, 1980; Sabatés & Saiz, 2000). Until now, taxonomical identification has not been detailed to the developmental stage of the main prey contributing to the diet of fish larvae and was rather limited to classifying prey into nauplii and copepodites for a given species. In addition, the overall structure of planktonic food webs varies considerably depending on the ecosystem and latitude, making it difficult to compare larval prey selectivity among regions.

The objective of this study was to compare the diet of 11 larval fish species of various morphology (4 orders and 8 families). In contrast to Shirota (1970) and Pearre (1986), all larval specimens considered in the present study were caught in the same plankton assemblage (i.e., at the same time and place) in the southern Gulf of St. Lawrence (Magdalen Islands region) and thus simultaneously feeding on prey present in the same zooplankton assemblage. We also compared the overlap of food niches among species. This study further aimed to improve our knowledge of the importance of morphological characteristics in determining feeding success during a critical life history stage for survival. Based on the food resource available in the prey field at the time of capture, we evaluated the feeding selectivity for each species. We investigated the extent to which the trophic niche in terms of prey diversity and size was related to variability in morphological traits among species. Given the high ichthyoplanktonic diversity that characterizes Magdalen Shelf waters (de Lafontaine *et al.*, 1991; White & Johns, 1997), this area constitutes an interesting model to gain a better understanding of the processes that regulate larval survival and better predict the responses of early life stages of fish to spatio-temporal variations in prey availability.

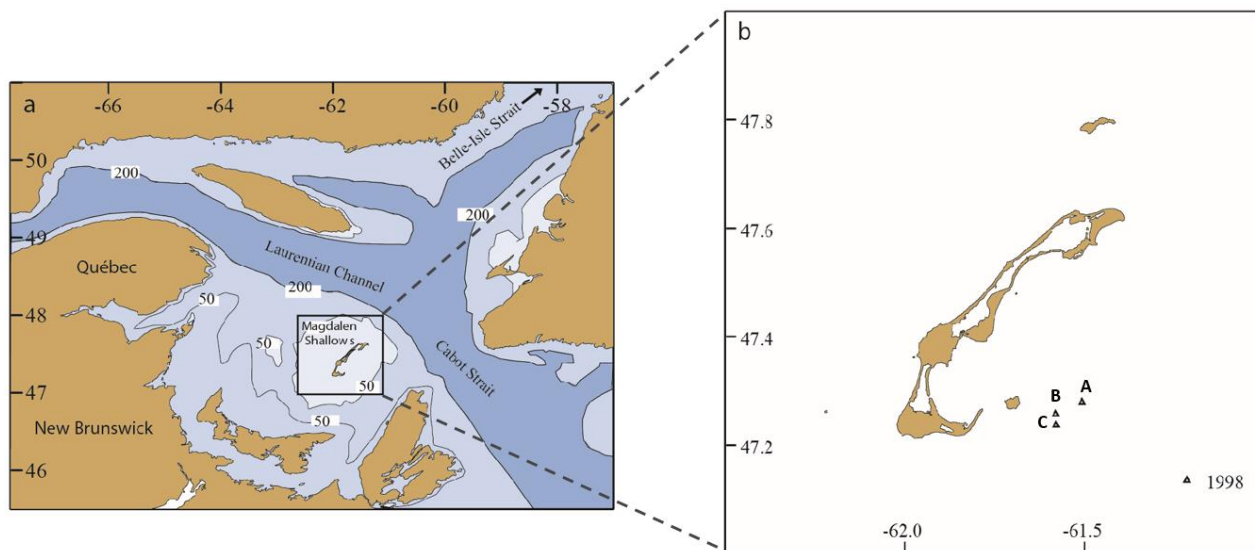
## 2.2 MATERIALS AND METHODS

### 2.2.1 Study area

The Gulf of St. Lawrence (GSL) is a large semi-enclosed sea connecting the St. Lawrence River to the Atlantic Ocean through the Strait of Belle Isle to the northeast and the Cabot Strait to the southeast. Given differences in bathymetric and oceanographic processes between the northern GSL (NGSL; Northwest Atlantic Fisheries Organization [NAFO] divisions 4R and 4S) and the southern GSL (SGSL; NAFO division 4T), the two regions are characterized by different biological community composition and overall productivity (Plourde & McQuinn, 2010).

The SGSL is a partially enclosed ecosystem (Hanson & Chouinard, 2002) comprising a broad shallow shelf (mostly < 50 m deep), the Magdalen Shallows, which is bordered to the north by the Laurentian Channel (Fig. 1a). Sampling for the present study was carried out in the Magdalen Islands region (Québec, Canada), a small archipelago of 200 km<sup>2</sup> comprising seven islands, located on a shallow 50 000 km<sup>2</sup> bank. The zooplanktonic community of the Magdalen Shallows differs from that of most of the Northwest Atlantic ecosystems. The larger copepods of the genus *Calanus* (*C. glacialis* and *C. hyperboreus*) are less common (Citarella, 1982; de Lafontaine *et al.*, 1991; Runge *et al.*, 1999), and the system is dominated by the smaller cyclopoid copepods (*Oithona similis*) and medium-sized calanoid copepods mainly represented by *Pseudocalanus* spp., *Temora longicornis*, *Centropages* sp., *Tortanus* sp., and *Acartia* sp. These characteristics make the Magdalen Shallows a favorable area for the rapid development of the larval stage of numerous fish species that feed mainly on various developmental stages of copepods. According to de Lafontaine *et al.* (1991) and White & Johns (1997), the highest ichthyoplankton production and diversity in the entire Gulf are found on the Magdalen Shallows. The system hosts one of the main spawning grounds for the Northwest Atlantic mackerel (*Scomber scombrus*) stock, and for several other commercially important fish species such as Atlantic cod (*Gadus*

*morhua*), yellowtail flounder (*Limanda ferruginea*), American plaice (*Hippoglossoides platessoides*), radiated shanny (*Ulvaria subbifurcata*) capelin (*Mallotus villosus*), sand lance (*Ammodytes* spp.) and Atlantic herring (*Clupea harengus*) (Grégoire *et al.*, 2014).



**Fig. 1.** (a) Location of the Magdalen Shallows in the southern Gulf of St. Lawrence with isobaths in metres; (b) Sampling stations where ichthyoplankton and zooplankton samples were captured on July 8, 1998.

### 2.2.2 Sampling procedures of fish larvae and their prey

Fish larvae used in this study were collected as part of a larger program carried out in the southeastern areas of the Magdalen Islands from July to August of four consecutive years (1997-2000) in one-day surveys conducted on a weekly basis (Robert *et al.*, 2008). To conduct a comparison of larval fish trophodynamics among a maximum number of fish species captured simultaneously during their early larval stage (pre-flexion), we focused on 3 stations sampled on July 8, 1998, when larval densities and diversity were the highest (Fig. 1b). These 3 stations comprised a total of 11 co-occurring species characterized by a wide diversity of morphological features. Larval fish considered in the present study included flatfish species from the families Pleuronectidae (yellowtail flounder *Limanda ferruginea*, winter flounder *Pseudopleuronectes americanus* and witch flounder *Glyptocephalus*

*cynoglossus*) and Bothidae (windowpane flounder *Scophthalmus aquosus*); five perciform species (Acanthopteri) from the families Stichaeidae (radiated shanny *Ulvaria subbifurcata* and Arctic shanny *Stichaeus punctatus*), Labridae (cunner *Tautogolabrus adspersus*), Scombridae (Atlantic mackerel *Scomber scombrus*) and Ammodytidae (sand lance *Ammodytes* sp.); one osmeriform from the family Osmeridae (capelin *Mallotus villosus*); and one gadiform from the family Gadidae (Atlantic cod *Gadus morhua*).

Sampling procedures were extensively described in Robert *et al.* (2007, 2008). Briefly, sampling of fish larvae was carried out using two 1 m<sup>2</sup> mouth aperture, 750 µm mesh nets attached to a rectangular frame. Two General Oceanic® flowmeters were placed within the mouth of each net to measure the volume of water filtered. Two smaller 81 cm<sup>2</sup> nets of 64 µm mesh size were also attached to the frame to capture concurrently at each sampling station the whole range of small mesozooplankton prey typically ingested by early larval stages of fish. The nets were towed obliquely at a vessel speed of 2 kt from the sea surface to a maximum depth corresponding to 5 m above the bottom. As fish larvae are visual particulate feeders (Greene, 1985), foraging on prey present in the upper layers during the day (Sabatés & Saiz, 2000; Govoni *et al.*, 1986; Grave, 1981), the 3 stations considered were sampled during daylight hours. For each tow, the sampled specimens were immediately immersed in a solution of tricaine methane sulfonate (MS-222) to minimize the risk of regurgitation, and fixed in 95% ethyl alcohol immediately after capture. Zooplankton samples from the 64 µm mesh nets were preserved in a 4% buffered formaldehyde solution for further taxonomical identification.

### **2.2.3 Laboratory analyses**

In the laboratory, all fish larvae were identified to the lowest taxonomic level possible, before being preserved in 95% ethyl alcohol. In September 2020, the quality of the preservation was confirmed and stomach content analysis was performed on a sub-sample of all species represented by at least 5 individuals from the same sampling station. Each sub-

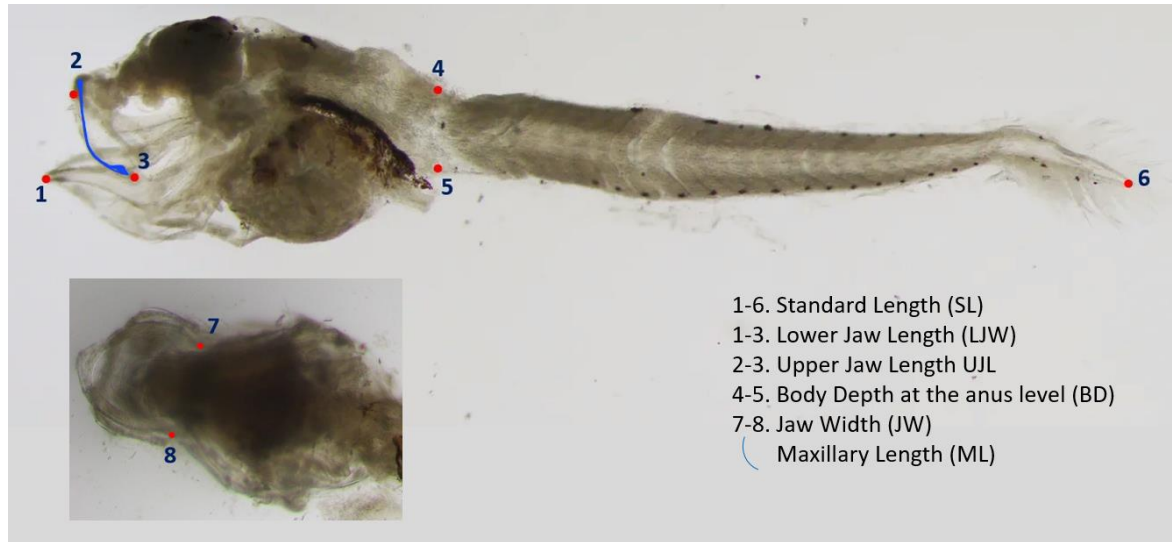
sample was composed of 5 to 10 specimens randomly selected for each species. A total number of 247 larvae have been analyzed for gut content (82, 81 and 84 larvae in station A, B and C, respectively).

To investigate potential morphological drivers of diet and prey selectivity among species, we recorded a suite of morphological characteristics in each specimen considered for gut content analysis (Fig. 2). We measured (1) larval standard length SL, (2) body depth at the anus level BD, (3) jaw width JW, (4) upper jaw length UJL, (5) lower jaw length LJW, and (6) right maxillary length RML, and (7) left maxillary length LML. SL and BD were determined to the nearest 0.05 mm at 20× magnification. Other mouth parameters were measured with an accuracy of 0.01 mm at 63-100× magnification. All measurements were taken using an Olympus SZX16 stereoscopic microscope coupled to the cellSens® image analysis software through an Olympus DP27 5MP colour camera. In some larvae, ML could not be precisely measured due to damage to the mouth structures.

The digestive tract of each larva was examined under an Olympus SZX16 stereoscopic microscope at ×110 magnification, coupled to the cellSens® image analysis software through an Olympus DP27 5MP colour camera. It was first separated from the body of the larva using fine dissecting needles and placed on a glass slide with a small amount of glycerol solution. The presence or absence of a yolk sac and the degree of digestion of stomach contents were noted. Each prey detected in the stomach was photographed, measured for total or prosome length (Uye, 1982) and identified to the lowest taxonomic level possible based on their size and specific morphological characteristics. Due to distortions caused by partial digestion, the developmental stage of some ingested prey could not be reliably identified. Those prey were assigned to stage in proportion to the relative abundance of identified taxa in the diet of the larva and were assigned measurements based on the average length of the corresponding developmental stage. Copepod eggs were considered prey due to their selection by several larval species, with the exception of egg sacks due to passive ingestion through the predation on females of egg-carrying copepod species such as *Oithona*

*similis*, *Pseudocalanus* sp., *Microcalanus pusillus* and *Microsetella* sp. Copepod egg identification was based on the following diameter values reported by McLaren *et al.* (1988), Castellani *et al.* (2005) and Demontigny *et al.* (2012): 135-165  $\mu\text{m}$  for *Calanus finmarchicus*, 165-195  $\mu\text{m}$  for *C. glacialis* and *Metridia longa*, and 195-250  $\mu\text{m}$  for *C. hyperboreus*. The measurement of each prey was converted to carbon mass from specific published length-weight and carbon-weight relationships (Table 3 in Bouchard *et al.*, 2016 and Table 1 in Robert *et al.*, 2008). Species-specific relationships were used when available. Otherwise, carbon content was estimated with general equations for closely related taxa (Annex Table AII). Total carbon consumed was calculated for each larva at each station. The richness of the diet of each larva was estimated based on the number of taxa found in the stomach. Copepod nauplii and copepodites were considered to contribute separately to the richness of the larva's diet because they do not generally have the same swimming and mobility performances, nor the same escape mechanisms, and thus may require different feeding and hunting strategies on the part of the larva.

To assess prey selectivity by fish larvae, precise information of the zooplankton abundance in the field at each station is needed. Thus, zooplankton identification procedure was carried out for the 64  $\mu\text{m}$  mesh net samples from the three stations where larvae originated. The zooplankton samples were divided in two size fractions, sieved through a 200  $\mu\text{m}$  mesh and then the small and large fractions were both diluted in specified volumes of water. Successive known aliquots were taken with a Hensen-Stempel pipette and all zooplankton organisms were identified at 110 $\times$  magnification to the lowest taxonomic level and stage possible until a minimum count of 400 copepod copepodites stages was obtained. The total number of organisms identified including copepod eggs, copepod nauplii, diplostracans, bivalves, gastropods, etc., were 1237 (station A), 1263 (station B), and 1576 (station C).



**Fig. 2.** Morphometric characteristics measured in each larva considered for gut content analysis. Standard length (SL) was measured from the tip of the snout to the end of the notochord; body depth (BD) was measured as a perpendicular line from the dorsal edge of the notochord down to the anus (stomach size is not included in this measurement); lower jaw length (LJL) was measured from the articular-quadrato joint to the anterior most tip of the dentary; upper jaw length (UJL) was measured from the articular-quadrato joint to the anterior most tip of the premaxilla; jaw width (JW) is defined, in the ventral view, as the distance between left and right postero-ventral tips of the articular bones of the jaws; maxillary length (ML) was determined where one of the two maxillary right or left had formed and was clearly visible.

#### 2.2.4 Data analysis

Both intraspecific and interspecific changes in the range of prey sizes ingested were determined. The standard deviation of log-transformed mean prey length was calculated as estimator of the diet niche breadth (Pearre, 1986). Given the limited number of larvae analyzed for each species, we did not attempt grouping them into size classes. Diet niche breadth values were averaged across all larvae of the same species pooled for the 3 stations.

For larval fish prey taxa, copepod nauplii of stages N1-N3 and N4-N6, and copepodites of stages CI-CIII and CIV-CVI, were considered as four distinct taxa. Stomach contents and



zooplankton data were used to calculate Chesson's  $\alpha$  electivity index for each species (Chesson, 1978). This index is used to calculate prey selectivity of a given individual larva for each prey taxon  $j$  found in the diet:

$$\alpha_j = \frac{d_j/p_j}{\sum(d_i/p_i)}, \text{ for } i = 1, \dots, N$$

where  $N$  is the number of prey taxa considered,  $(d_j/p_j)$  is the ratio of the relative abundance of prey  $j$  in diet ( $d_j$ ) and in plankton ( $p_j$ ) and  $\sum(d_i/p_i)$  is the sum of this ratio for all prey taxa. Given the low overall number of *Ammodytes* sp. and *G. cynoglossus* captured and the limited number of prey detected in their stomachs, these two species were not considered in the calculation of  $\alpha$ . This index was calculated independently for each individual larva and then averaged for each species. Only prey taxa representing more than 2% of total carbon ingested at the 3 stations for a given larval fish species were considered in the calculation of  $\alpha$ . Selection is considered neutral when  $\alpha_j = 1/N$ . Concordantly,  $\alpha_j$  values higher than  $1/N$  indicate that prey taxon  $j$  was ingested in higher proportions than expected from their relative abundance in the potential prey field: this is referred to as positive selection for prey  $j$ . To the opposite,  $\alpha_j$  values smaller than  $1/N$  indicate a negative selection for prey  $j$ . Following Burns *et al.* (2020), selection was defined as strongly positive when Chesson's  $\alpha_j > 2/N$  (the proportion of prey  $j$  in the stomach was at least twice its proportion in the field), and strongly negative if it was less than  $1/2N$ .

The  $\alpha$  index was used because it is recognized as one of the most stable and robust indices to measure prey taxa preference independently of their density and the predator's hunting strategies (Lechowicz, 1982; Pearre, 1982; Govoni *et al.*, 1986). Digested prey that could not be identified were removed from calculations. In the present study, unknowns were rare exceptions; they only represented 0.73% of all prey ingested (0.54% nauplii, 0.12% copepodites and 0.07% other unidentified). In the rare case when a prey taxon found in a

larva's stomach was not observed in the environmental plankton fraction identified for a given station, it was assigned a default density of half of the lowest density among all taxa identified at that station (it only happened for *C. finmarchicus* N1-N3 in station A et B and *C. finmarchicus* N4-N6 in station B). The index was calculated for each individual larva and then averaged for each species across all stations. The interspecific variability of prey selectivity was assessed by comparing the average  $\alpha$  for each prey ingested by a given species.

To compare feeding niche overlap among species, the Schoener index (Schoener, 1968) was selected for its advantage of being independent of arbitrary classifications of unidentified prey species due to the advanced digestive activity of the larva, it facilitates intercommunity comparisons and it is known to be free of assumptions about competition processes (Abrams, 1980). According to Linton *et al.* (1981), the Schoener index is the most appropriate for estimating diet overlap of the various dietary overlap indices available. The index was calculated as:

$$C_{jk} = (1 - 1/2 \sum |P_{ij} - P_{ik}|) * 100$$

where  $C_{jk}$  is the feeding niche overlap between fish species  $j$  and  $k$ , and  $P_{ij}$  and  $P_{ik}$  are the relative abundance of prey type  $i$  in the diets of species  $j$  and  $k$ , respectively. The overlap is complete when  $C_{jk} = 100$  and absent when  $C_{jk} = 0$ . Schoener's index values are usually considered biologically significant when exceeding 60 (Zaret & Rand, 1971; Wallace, 1981).

Larvae with empty guts ( $n = 35$ ) were excluded from statistical analyses. A normal CLUSTER analysis with average linkage was performed on an Euclidean distance similarity matrix based on morphological characteristics data after standardization (Clarke, 1993). To compare variability in diet composition independent of larval size, morphological variables were standardized by dividing each parameter of the mouth (JW, mean UJL-LJL and mean RML-LML) as well as BD on the standard length (SL). Revealed clusters of species of

similar morphologies, were visualized with a non-metric multidimensional scaling (nMDS) analysis (version 6.1.6, PRIMER-E). As the nMDS is an ordination method and does not include any direct tool for statistical testing, we applied a non-parametric test ANOSIM (**AN**alysis **O**f **S**IMilarity) to determine statistical differences among morphological species groups.

To test whether groups of morphologically similar species feed on the same prey taxa, a nMDS analysis was performed on a Bray-Curtis similarity matrix based on untransformed data of the average number of each prey taxa ingested by each species (Clarke, 1993). The ANOSIM was used to measure differences between a priori defined groups of morphologically similar species.

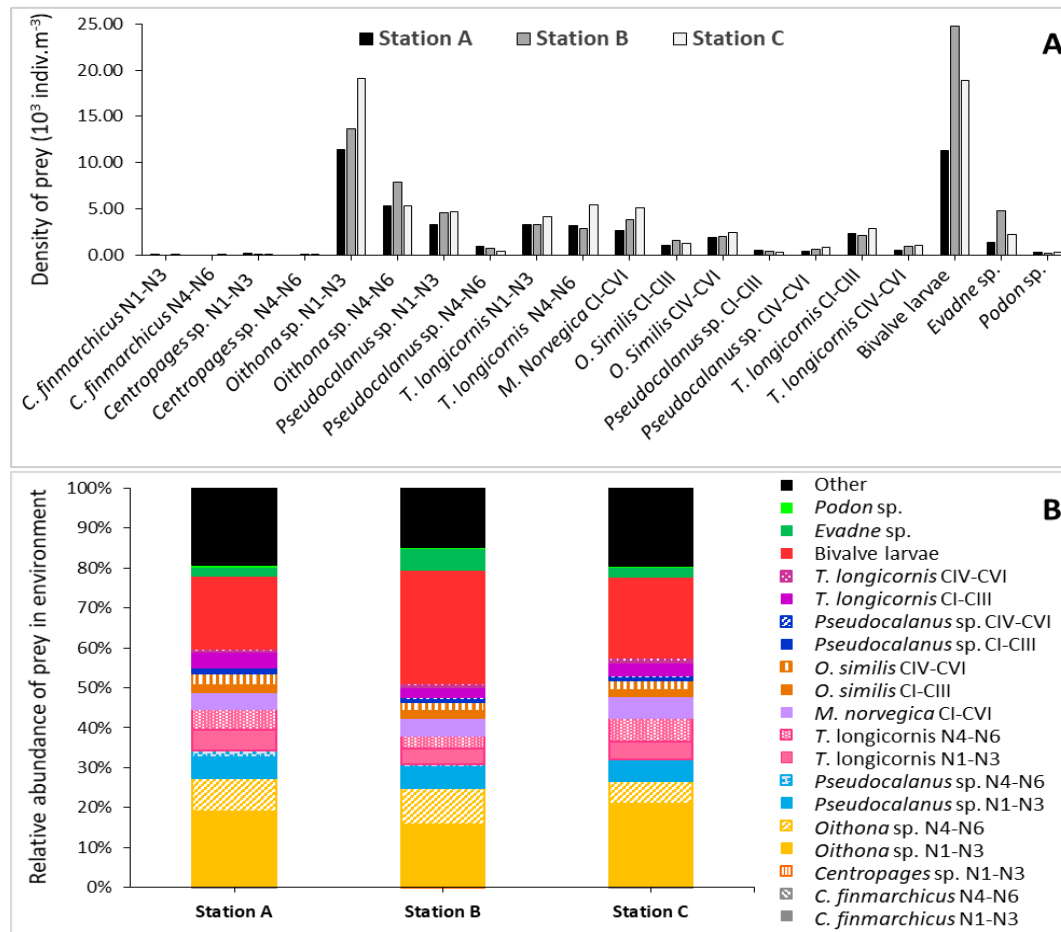
## 2.3 RESULTS

### 2.3.1 Potential prey field

Zooplankton composition was similar among the three stations, with moderate variability in the density and relative abundance of taxa. In terms of density and abundance, cyclopoid nauplii stages of *Oithona* sp. (mostly *O. similis*) were numerically dominant in the zooplankton assemblage at all three stations (Fig. 3A, B). The proportions of younger nauplii stages (N1-N3) of *Oithona* sp. were higher than that for the advanced stages (N4-N6) by coefficients of 2.15, 1.73 and 3.62 at station A, B and C, respectively (Fig. 3B). *Pseudocalanus* sp. nauplii were characterized by higher abundance of N1-N3 relative to N4-N6 stages at the three stations. Nauplii stages N1-N3 of *Pseudocalanus* sp. were 3.36, 5.89 and 12.12 times more abundant than N4-N6 stages at stations A, B and C, respectively. In addition, *Pseudocalanus* sp. N1-N3 were similar in proportion at all the stations (5.04 to 5.25%) compared to their older conspecifics (N4-N6) which presented variable proportions

among stations (0.42 to 1.56%). Similarly, N1-N3 and N4-N6 stages of *Temora* sp. nauplii occurred in equal proportions at the three stations. The abundance of nauplii and copepodites of the large calanoid copepod *Calanus finmarchicus* was very low at all three stations. Nauplii of *C. finmarchicus* N1-N3 were present in both stations A and C with relative abundances of 0.21% and 0.10%, respectively. However, the advanced stages of *C. finmarchicus* nauplii (N4-N6) were only available at station C with a very low proportion (0.03%). Copepodites were relatively less abundant in the environment than nauplii (14.69% of total potential prey versus 44.23% for nauplii). Copepodites of the harpacticoid *Microsetella norvegica* CI-CVI were the most abundant, followed by young stages CI-CIII of *Temora longicornis* and advanced stages (CIV-CVI) of *Oithona similis*. All non-copepod potential prey represented less than 2.0% of all organisms at each station.

Diplostraca availability varied among stations but was generally high at station B (Fig. 3B). This is due to *Evadne* sp. which represented a considerable portion of the zooplankton at that station (5.43% of all prey by numbers) compared to the other two stations A and C, which showed similar lower proportions (2.27% and 2.39% respectively). Bivalve larvae reached particularly high densities and proportions at station B (24,784 ind. m<sup>-3</sup> and 28.42%, respectively) compared to the other two stations.



**Fig. 3.** (A) Densities of frequently consumed prey taxa at collection stations, and (B) Relative abundance of common prey field taxa in the environment.

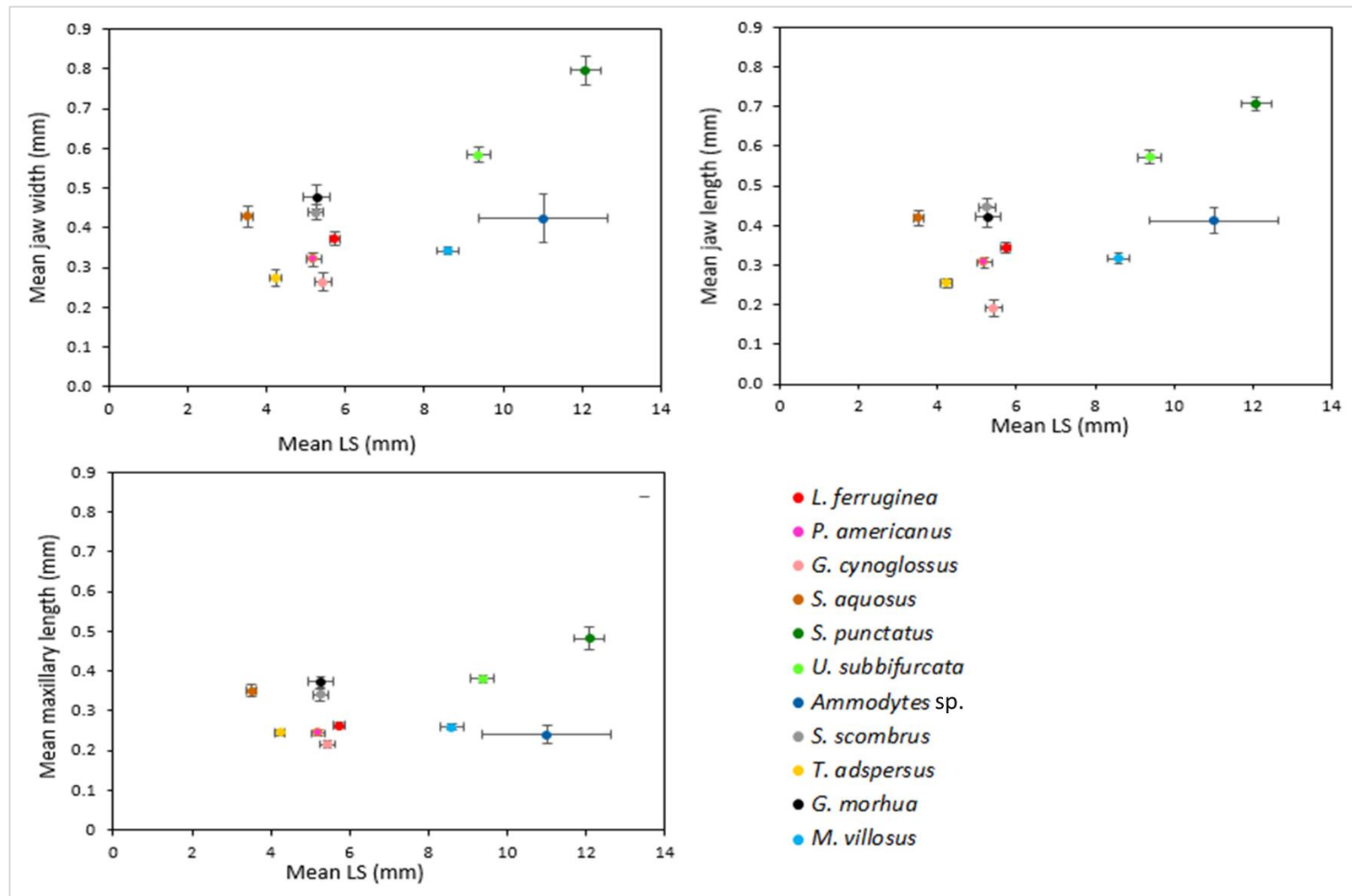
### 2.3.2 Larval species characteristics

The larvae dissected in this study measured on average  $6.69 \text{ mm} \pm 2.98$  (Table 1). The smallest larvae on average were observed in the pleuronectiform *Scophthalmus aquosus* ( $3.51 \pm 0.70$ ) and the largest larvae in the perciform *Stichaeus punctatus* ( $12.08 \pm 1.94$ ). Mean jaw width (JW) varied from  $0.26 \pm 0.02$  to  $0.80 \pm 0.04$  mm, and mean jaw length (JL) varied from  $0.19 \pm 0.02$  to  $0.71 \pm 0.02$ . Mean JW and mean JL corresponded to 3.84 to 12.20 % mean SL and 3.53 to 11.94 % mean SL, respectively. None of the larvae dissected in this study were yolk-sac larvae. All larvae were approximately at the same developmental stage (pre-flexion stage), identified here by the absence of the folding and hypural plates at the end of the notochord.

The relationship between mouth parameters and standard length (SL) varied among species (Fig. 4). The three species of different morphologies *Scomber scombrus* (perciform), *Gadus morhua* (gadiform) and *Scophthalmus aquosus* (pleuronectiform) had on average the widest jaws relative to body size (8.35, 9.06 and 12.20% of body size, respectively) as well as the longest jaws (8.00, 8.47 and 11.94% of body size, respectively). At the other extreme *Glyptocephalus cynoglossus* (pleuronectiform), *Mallotus villosus* (osmeriform) and *Ammodytes* sp. (perciform) had the narrowest (3.48, 3.98 and 4.85%, respectively) and the smallest jaws relative to body size (3.53, 3.69 and 3.74%, respectively). When mouth parameters were compared among species, the two Stichaeidae (perciformes) *Stichaeus punctatus* and *Ulvaria subbifurcata* showed on average the greatest JW ( $0.80 \pm 0.04$ , and  $0.58 \pm 0.02$ , respectively), JL ( $0.71 \pm 0.02$  and  $0.57 \pm 0.02$ , respectively) and maxilla at size ( $0.48 \pm 0.03$  and  $0.38 \pm 0.01$ , respectively). The smallest mouth was recorded in *G. cynoglossus* ( $0.26 \pm 0.02$  for JW;  $0.19 \pm 0.02$  for JL and  $0.22 \pm 0.01$  for maxilla). The maxilla, which extends along the upper jaw, corresponded to 54.94– 95.63% JL (mean UJL-LJL) for all species except for *G. cynoglossus* (111.58%). Mean maxilla of *Ammodytes* sp. corresponded only to 2.18% mean SL, however it reached 9.96% for *Scophthalmus aquosus*.

**Table 1.** Mean size  $\pm$  standard deviation of morphometric characteristics of each larval species (SL= standard length; BD = body depth; JW = jaw width; UJL= upper jaw length; LJL= lower jaw length and ML= maxillary length).

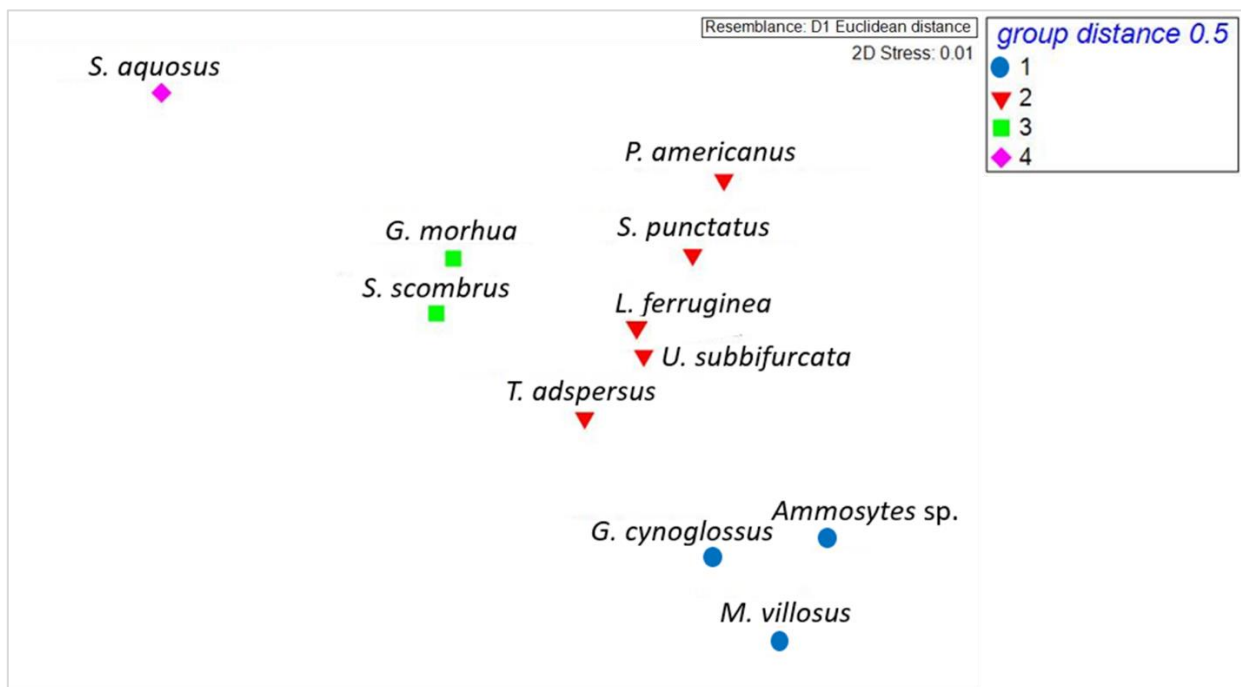
Species	Range SL (mm)	SL (mm)	BD (mm)	JW ( $\mu$ m)	UJL ( $\mu$ m)	LJL ( $\mu$ m)	Right and left ML ( $\mu$ m)
<i>L. ferruginea</i>	4.36 - 7.05	5.73 $\pm$ 0.73	0.50 $\pm$ 0.15	372.17 $\pm$ 97.42	387.73 $\pm$ 70.21	299.67 $\pm$ 77.96	261.64 $\pm$ 41.98
<i>P. americanus</i>	3.76 - 6.85	5.19 $\pm$ 0.93	0.66 $\pm$ 0.30	320.52 $\pm$ 82.81	336.07 $\pm$ 82.06	275.41 $\pm$ 62.50	241.32 $\pm$ 43.67
<i>G. cynoglossus</i>	4.79 - 6.02	5.43 $\pm$ 0.44	0.29 $\pm$ 0.05	263.17 $\pm$ 50.06	175.87 $\pm$ 46.38	207.36 $\pm$ 78.89	213.81 $\pm$ 44.80
<i>S. aquosus</i>	2.43 - 5.2	3.51 $\pm$ 0.70	0.33 $\pm$ 0.11	428.42 $\pm$ 139.08	457.02 $\pm$ 125.30	381.57 $\pm$ 91.74	353.10 $\pm$ 78.55
<i>S. punctatus</i>	9.67 - 16.83	12.08 $\pm$ 1.94	1.32 $\pm$ 0.27	795.91 $\pm$ 182.89	736.85 $\pm$ 109.82	676.15 $\pm$ 76.48	479.02 $\pm$ 134.09
<i>U. subbifurcata</i>	6.56 - 12.06	9.38 $\pm$ 1.75	0.80 $\pm$ 0.16	583.58 $\pm$ 116.93	593.90 $\pm$ 112.06	549.88 $\pm$ 123.79	380.65 $\pm$ 62.35
<i>Ammodytes</i> sp.	8.59 - 17.37	11.02 $\pm$ 3.65	0.61 $\pm$ 0.28	423.45 $\pm$ 137.81	415.45 $\pm$ 115.93	408.60 $\pm$ 40.59	226.38 $\pm$ 39.56
<i>S. scombrus</i>	2.88 - 6.90	5.26 $\pm$ 1.09	0.40 $\pm$ 0.12	438.74 $\pm$ 105.34	480.31 $\pm$ 137.34	410.18 $\pm$ 115.86	344.70 $\pm$ 88.27
<i>T. adspersus</i>	2.92 - 5.13	4.23 $\pm$ 0.61	0.29 $\pm$ 0.08	273.56 $\pm$ 88.47	267.51 $\pm$ 61.73	242.05 $\pm$ 50.65	243.65 $\pm$ 31.82
<i>G. morhua</i>	3.24 - 9.95	5.27 $\pm$ 1.74	0.46 $\pm$ 0.20	477.53 $\pm$ 153.84	469.93 $\pm$ 155.86	373.50 $\pm$ 119.43	368.81 $\pm$ 66.21
<i>M. villosus</i>	5.98 - 10.60	8.59 $\pm$ 1.28	0.27 $\pm$ 0.06	342.08 $\pm$ 43.83	331.47 $\pm$ 74.05	302.16 $\pm$ 56.02	258.71 $\pm$ 42.27



**Fig. 4.** Comparison of morphometric relationships of mouth gape (jaw width, jaw length and maxillary in mm) and body length (in mm) for larval species.



The various species of fish larvae displayed conspicuous morphological differences that were reflected in non-metric MDS analysis of similarities of morphometric characteristics (Fig. 5). The ANOSIM test discriminated four groups of highly differentiated species which are all distinguished by an  $R > 0.8$ . The two forage species *Ammodytes* sp. and *M. villosus* characterized by a small jaw width relative to body length and a linear intestinal morphology formed with the small, elongated but narrow flatfish *G. cynoglossus* a single group. Atlantic mackerel and Atlantic cod, which are characterized by an anteriorly deep bodied shape with large mouth gape width relative to body length, formed a second group. The third group containing the two Stichaeidae *U. subbifurcata* and *S. punctatus* with a stocky, moderately elongated body, as well as the two pleuronectiformes *L. ferruginea*, *P. americanus* and the perciform *T. adspersus*. The pleuronectiform *S. aquosus* with a diamond-shaped body formed another separate group in itself.



**Fig. 5.** Result of the non-metric MDS analysis of similarities of morphometric characteristics of larval species.

### 2.3.3 Larval fish trophodynamics

#### 2.3.3.1 Diet composition

Larvae dissected in the present study fed most frequently on copepod nauplii. The perciform *S. scombrus* consumed the most prey on average (47.77%), followed by the pleuronectiform *S. aquosus* (29.19%) and the gadiform *G. morhua* (21.07%) (Table 2). Both Stichaeidae *S. punctatus* and *U. subbifurcata* consumed on average the same number of prey items (8.94% and 8.81%, respectively) (Table 2) but not the same mean amount carbon ingested (0.21 and 0.36  $\mu\text{g C}$ , respectively) (Table 3). With the exception of *G. cynoglossus*, pleuronectiform species (*L. ferruginea*, *P. americanus* and *S. aquosus*) all presented the lowest proportions of larvae with empty stomachs, comprising between 0 and 7.69% of the total number of larvae analysed for each species (Table 2).

*Pseudocalanus* sp. and *Oithona* sp. were the main prey of most larval species (Table 2). The only exceptions to this pattern were observed for *M. villosus* and *L. ferruginea*, which fed mainly on *T. longicornis* nauplii (47.86 and 30.50% of prey numbers in the diet, respectively). In three out of five perciforms (*U. subbifurcata*, *Ammodytes* sp. and *S. scombrus*), *Pseudocalanus* sp. nauplii remained the dominant prey in terms of numbers and carbon content.

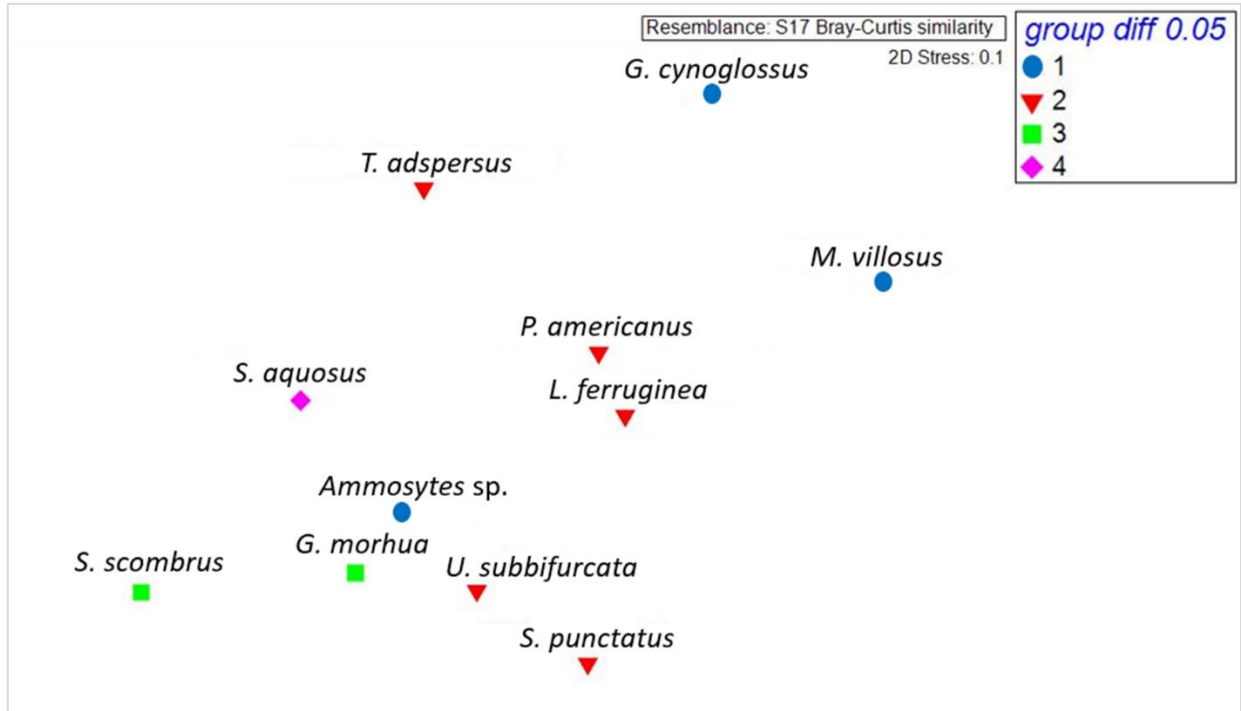
**Table 2.** Diet composition of larval species expressed as the percent contribution by numbers of the different prey taxa.

Prey taxon	Larval species										
	Pleuronectiforme				Perciforms					Gadiform	Osmeriform
	<i>L. ferruginea</i>	<i>P. americanus</i>	<i>G. cynoglossus</i>	<i>S. aquosus</i>	<i>S. punctatus</i>	<i>U. subbifurcata</i>	<i>Ammodytes</i> sp.	<i>S. scombrus</i>	<i>T. adspersus</i>	<i>G. morhua</i>	<i>M. villosus</i>
Copepods											
Eggs (<135 µm)	0.22	0.35	—	0.17	—	—	—	0.34	—	2.19	—
Nauplii											
<i>Acartia</i> sp. N1-N3	—	—	—	—	1.32	—	—	—	—	—	—
<i>Acartia</i> sp. N4-N6	—	—	—	—	1.32	0.37	—	—	—	—	—
<i>C. finmarchicus</i> N1-N3	—	—	—	0.23	1.41	6.31	1.32	—	—	0.46	—
<i>C. finmarchicus</i> N4-N6	—	0.22	—	0.44	0.13	0.83	—	0.32	—	0.31	—
<i>Centropages</i> sp. N1-N3	—	—	—	0.07	2.63	3.26	—	0.49	—	—	—
<i>Oithona</i> sp. N1-N3	6.18	13.44	43.75	29.68	—	3.87	23.37	20.51	56.00	11.81	10.71
<i>Oithona</i> sp. N4-N6	6.51	1.68	25.00	5.11	8.32	22.95	25.53	15.16	30.86	5.61	9.94
<i>Microcalanus</i> sp.	—	—	—	—	—	0.19	—	—	—	—	—
<i>Microsetella</i> sp. N1-N6	0.60	—	—	0.72	—	—	—	—	—	—	—
<i>Pseudocalanus</i> sp. N1-N3	19.67	16.03	18.75	12.26	24.93	31.63	35.12	44.26	13.14	30.31	9.17
<i>Pseudocalanus</i> sp. N4-N6	12.54	7.52	12.50	4.00	20.15	23.97	11.57	12.25	—	29.65	11.61
<i>T. longicornis</i> N1-N3	11.95	13.22	—	15.63	0.40	—	—	3.95	—	1.39	8.93
<i>T. longicornis</i> N4-N6	30.50	9.52	—	19.60	0.42	—	—	2.24	—	1.33	47.86
Copepodites											
<i>Microcalanus</i> sp. CI-CVI	0.45	—	—	—	0.11	—	—	—	—	—	—
<i>M. norvegica</i> CI-CVI	0.26	6.47	—	3.28	—	—	—	—	—	—	—
<i>O. similis</i> CI-CIII	—	—	—	—	1.09	2.51	3.10	—	—	1.43	—
<i>O. similis</i> CIV-CVI	—	—	—	—	18.87	1.63	—	—	—	1.15	—
<i>Pseudocalanus</i> sp. CI-CIII	0.45	—	—	—	—	0.28	—	0.04	—	1.63	—
<i>Pseudocalanus</i> sp. CIV-CVI	—	—	—	—	—	—	—	—	—	3.35	—
<i>T. longicornis</i> CI-CIII	8.49	4.12	—	5.20	1.53	1.48	—	0.29	—	2.52	1.79
<i>T. longicornis</i> CIV-CVI	—	—	—	0.53	—	0.72	—	—	—	—	—
Diplostracans											
<i>Evadne</i> sp.	0.40	11.42	—	—	17.11	—	—	0.11	—	1.18	—
<i>Podon</i> sp.	—	1.39	—	—	0.26	—	—	—	—	0.86	—
Gastropods	0.16	—	—	1.26	—	—	—	—	—	—	—
Bivalve larvae	1.65	14.61	—	1.82	—	—	—	—	—	4.70	—
Fish larvae	—	—	—	—	—	—	—	0.03	—	—	—
Number of larvae analysed	30	26	5	27	26	30	5	30	19	29	20
Mean number of prey	10.07	7.73	1.6	29.19	8.81	8.94	12.2	47.77	4.74	21.07	2.45
Number of empty stomachs (% empty)	2 (6.67)	2 (7.69)	1 (20)	0 (0)	7 (26.92)	12 (40)	1 (20)	0 (0)	4 (21.05)	0 (0)	6 (30)
Feeding incidence (%)	93.33	92.31	80	100	73.08	60	80	100	78.95	100	70

**Table 3.** Diet composition of larval species expressed as the percent contribution by carbon ingested of the different prey taxa.

Prey taxon	Larval species										
	Pleuronectiformes				Perciformes					Gadiform	Osmeriform
	<i>L. ferruginea</i>	<i>P. americanus</i>	<i>G. cynoglossus</i>	<i>S. aquosus</i>	<i>S. punctatus</i>	<i>U. subbifurcata</i>	<i>Ammodytes</i> sp.	<i>S. scombrus</i>	<i>T. adspersus</i>	<i>G. morhua</i>	<i>M. villosus</i>
Copepods											
Eggs (<135 µm)	0.02	0.02	—	0.02	—	—	—	0.15	—	0.77	—
Nauplii											
<i>Acartia</i> sp. N1-N3	—	—	—	—	0.67	—	—	—	—	—	—
<i>Acartia</i> sp. N4-N6	—	—	—	—	0.23	1.40	—	—	—	—	—
<i>C. finmarchicus</i> N1-N3	—	—	—	0.37	7.67	4.77	6.71	—	—	0.78	—
<i>C. finmarchicus</i> N4-N6	—	1.68	—	3.53	1.00	5.41	—	4.58	—	0.64	—
<i>Centropages</i> sp. N1-N3	—	—	—	0.08	0.30	2.16	—	1.20	—	—	—
<i>Oithona</i> sp. N1-N3	0.93	2.62	27.99	4.27	—	0.36	5.99	3.85	37.10	1.66	0.93
<i>Oithona</i> sp. N4-N6	2.05	0.63	10.09	2.21	0.57	5.35	15.00	8.62	36.24	1.91	3.75
<i>Microcalanus</i> sp.	—	—	—	—	—	0.05	—	—	—	—	—
<i>Microsetella</i> sp. N1-N6	0.28	—	—	0.33	—	—	—	—	—	—	—
<i>Pseudocalanus</i> sp. N1-N3	10.44	8.00	31.03	7.88	11.71	26.60	39.09	54.46	26.66	19.49	6.69
<i>Pseudocalanus</i> sp. N4-N6	9.61	6.41	30.90	5.98	13.90	24.72	27.94	19.03	—	26.36	5.87
<i>T. longicornis</i> N1-N3	7.99	9.17	—	9.45	0.31	—	—	2.58	—	0.94	9.79
<i>T. longicornis</i> N4-N6	51.57	22.46	—	34.74	1.33	—	—	4.44	—	2.25	70.77
Copepodites											
<i>Microcalanus</i> sp. CI-CVI	0.20	—	—	—	0.19	—	—	—	—	—	—
<i>M. norvegica</i> CI-CVI	0.42	3.12	—	6.20	—	—	—	—	—	—	—
<i>O. similis</i> CI-CIII	—	—	—	—	1.43	3.45	5.28	—	—	1.08	—
<i>O. similis</i> CIV-CVI	—	—	—	—	35.09	5.73	—	—	—	5.55	—
<i>Pseudocalanus</i> sp. CI-CIII	0.36	—	—	—	—	0.29	—	0.14	—	3.95	—
<i>Pseudocalanus</i> sp. CIV-CVI	—	—	—	—	—	—	—	—	—	18.84	—
<i>T. longicornis</i> CI-CIII	14.75	7.31	—	12.21	9.59	10.24	—	0.64	—	5.49	2.21
<i>T. longicornis</i> CIV-CVI	—	—	—	7.51	—	9.47	—	—	—	—	—
Diplostracans											
<i>Evadne</i> sp.	0.08	32.14	—	—	16.42	—	—	0.31	—	6.19	—
<i>Podon</i> sp.	—	2.74	—	—	0.20	—	—	—	—	0.58	—
Gastropods	0.07	—	—	0.58	—	—	—	—	—	—	—
Bivalve larvae	1.23	3.70	—	4.67	—	—	—	—	—	3.50	—
Fish larvae	—	—	—	—	—	—	—	2.90	—	—	—
Number of larvae analysed	30	26	5	27	26	30	5	30	19	29	20
Mean carbon ingested (µg)	0.22	0.24	0.10	0.19	0.36	0.21	0.12	0.12	0.05	0.22	0.25

Based on morphological groups, there was no significant differentiation in the composition of stomach contents as revealed by an ANOSIM test (a very low  $R = 0.118$ ). The nMDS analysis revealed large variability in prey composition within groups of morphologically similar species (Fig. 6).



**Fig. 6.** Result of non-metric MDS analysis of similarities of stomach content of larval species.

Among all species except for *M. villosus*, the contribution of young stages of *Pseudocalanus* sp. N1-N3 (12.26- 44.26%) to the overall proportion of prey by numbers was always greater than that of *Pseudocalanus* sp. N4-N6 (4.00-29.65%). The contribution of *C. finmarchicus* nauplii to diet composition by numbers was relatively small and did not exceed 1.32% except for *U. subbifurcata*, for which *C. finmarchicus* N4-N6 represented 6.31%. Copepodites were rarely consumed overall, with the exception of CIV-CVI stages of *O. similis*, which represented up to 18.87% of the larval diet of *S. punctatus* by prey numbers (Table 2). *S. punctatus* also ingested large numbers of *Evadne* sp. (17.11% of prey by numbers). *Evadne* sp. and bivalvia contributed a significant fraction to the stomach content of larvae of *P. americanus*, representing together more than 26% of the diet in numbers. Although bivalves were the second most consumed prey by numbers in *P. americanus*, they contributed only 3.70% to the ingested carbon. *Evadne* sp. contributed the highest amount of carbon of any prey taxa in the *P. americanus* diet (32.14%).

With the exception of *G. cynoglossus*, N4-N6 stages of *T. longiconis* nauplii were the most important prey in terms of carbon for pleuronectiform and osmeriform larvae (Table 3), but only represented a small fraction of the total carbon ingested by perciform larvae. For most perciform species (*U. subbifurcata*, *Ammodytes* sp. and *S. scombrus*), carbon content was dominated by nauplii of *Pseudocalanus* sp., which contributed between 26.60% and 54.46% of the biomass. The perciform *S. punctatus* had the highest mean carbon ingested (0.36 µg), for which the relatively large *O. similis* CIV-CVI copepodites strongly dominated the carbon content (35.09%).

#### 2.3.3.2 Diet overlap index

Diet overlap index differed among species and varied with stations. A higher overlap, varying between 59.52 and 67.12%, was observed among pleuronectiform species. The degree of overlap was highly variable among perciform species. The lowest overlap was recorded between *S. punctatus* and *T. adspersus* (21.46%). A relatively high dietary overlap was observed between *U. subbifurcata* and the two species *S. scombrus* and *S. punctatus* (64.05 and 62.15, respectively).

We observed a moderate feeding niche overlap between pleuronectiform and perciform species (Fig. 7A). The only exception to this pattern occurred for the perciform *S. punctatus* and the pleuronectiform *S. aquosus*, which showed a low feeding niche overlap (24.16%). The pleuronectiform and perciform species were characterized by a moderate or high overlap index with the gadiform *G. morhua* and the osmeriform *M. villosus*. In the case of *G. morhua*, the overlap of feeding niches was high with the pleuronectiform *L. ferruginea* (52.04%) and the three perciform species *S. punctatus* (57.42%), *U. subbifurcata* (68.96%) and *S. scombrus* (63.88%); and moderate with the perciform *T. adspersus* (30.65%) and the two pleuronectiform *P. americanus* and *S. aquosus* (49.60 and 40.96%, respectively). *M. villosus* showed the same pattern with the perciform *T. adspersus* (29.82%) and the two pleuronectiformes *L. ferruginea* (74.66%) and *P. americanus* (49.31%) while the overlap became high with the pleuronectiform *S. aquosus* (59.30%) and low with the other perciform species.

Comparing the feeding niche overlap index based on stations revealed high variability at the station level for some species (Fig. 7B). Particularly low feeding niche overlap was observed between the pleuronectiform *P. americanus* at station B and all other species of the different stations except their conspecifics captured at station C (35.29%). Similarly, the overlap between the osmeriform *M. villosus* at station B and all perciform and gadiform species of the three stations was low. The overlap was strong between *S. scombrus*, *L. ferruginea* and *T. adspersus* at station B and their conspecifics at station C (92.19, 89.01 and 83.74%, respectively) and *S. aquosus*, *L. ferruginea* and *G. morhua* at station A with their conspecifics at station C (85.81, 79.93 and 76.30%, respectively).



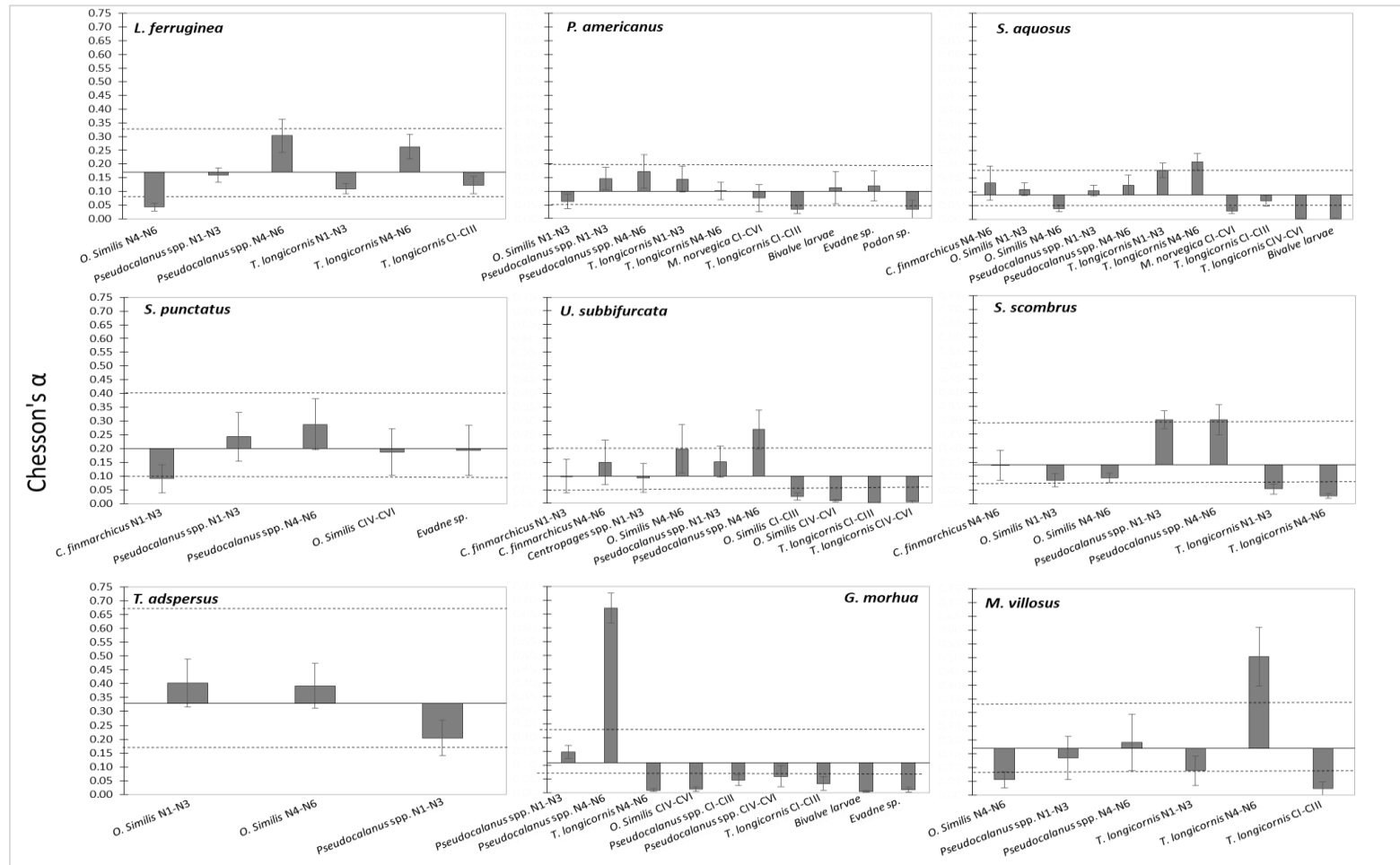


### 2.3.4 Prey selectivity

Fish species in the present study presented some common trends, showing stronger selection for copepod nauplii compared to copepodites (Fig. 8). However detailed selectivity patterns, described at the level of prey life stages, showed great variation among species. The majority of species showed a preference for *Pseudocalanus* sp. nauplii. *S. scombrus*, *G. morhua* and *S. punctatus* larvae did not exhibit positive preference for any of the commonly consumed prey taxa other than *Pseudocalanus* sp. nauplii. *S. scombrus* larvae strongly selected for both N1-N3 and N4-N6 stages of *Pseudocalanus* sp. Although diversity of ingested prey was high, the gadiform *G. morhua* showed a very strong positive selectivity for only N4-N6 stages of *Pseudocalanus* sp. Strong positive selection for *Pseudocalanus* sp. N4-N6 was also observed in the perciform *U. subbifurcata*. The two species *G. morhua* and *U. subbifurcata* revealed moderate positive selection for N1-N3 stages of *Pseudocalanus* sp. The only species that showed a negative selectivity against *Pseudocalanus* sp. nauplii, more precisely N4-N6 stages, was the perciform *T. adspersus*. In return, it positively selected for all nauplii stages of *O. similis*. The diet of *T. adspersus* was restricted to these two prey species. For three species, feeding selectivity was oriented towards both *Pseudocalanus* sp. and *T. longicornis* nauplii. Positive selection for these prey items was noted for the two pleuronectiforms *P. americanus* and *S. aquosus*. The selectivity for N4-N6 stages of *T. longicornis* was strong for *S. aquosus* and almost neutral for *P. americanus*. *L. ferruginea* selected positively for the advanced nauplii (N4-N6) of *Pseudocalanus* sp. and *T. longicornis*, whereas the younger stages N1-N3 were negatively selected. *M. villosus* showed high selection only for the nauplii N4-N6 of *T. longicornis*.

In contrast, *S. scombrus* and *G. morhua* larvae demonstrated a strong negative selection against *T. longicornis* nauplii. The selectivity of the most abundant copepod prey in the environment, *O. similis* nauplii, was negative for all species except for the two perciformes *T. adspersus* (neutral selectivity) and *U. subbifurcata* (positive). Selectivity for the large calanoid nauplii of *C. finmarchicus* was variable among species: positive selectivity for N4-N6 stages by *S. aquosus*, very strong negative selectivity against N1-N3 stages by *S. punctatus* and neutral selectivity for N1-N3 and N4-N6 stages by *U. subbifurcata* and *S. scombrus*, respectively. The

larval species of the present study exhibited a negative or neutral selectivity for larger prey mainly represented by bivalve larvae, Diplostraca (*Evadne* sp. and *Podon* sp.) and copepodites stages such as *Pseudocalanus* sp., *T. longicornis*, *O. similis* and *M. norvegica*.



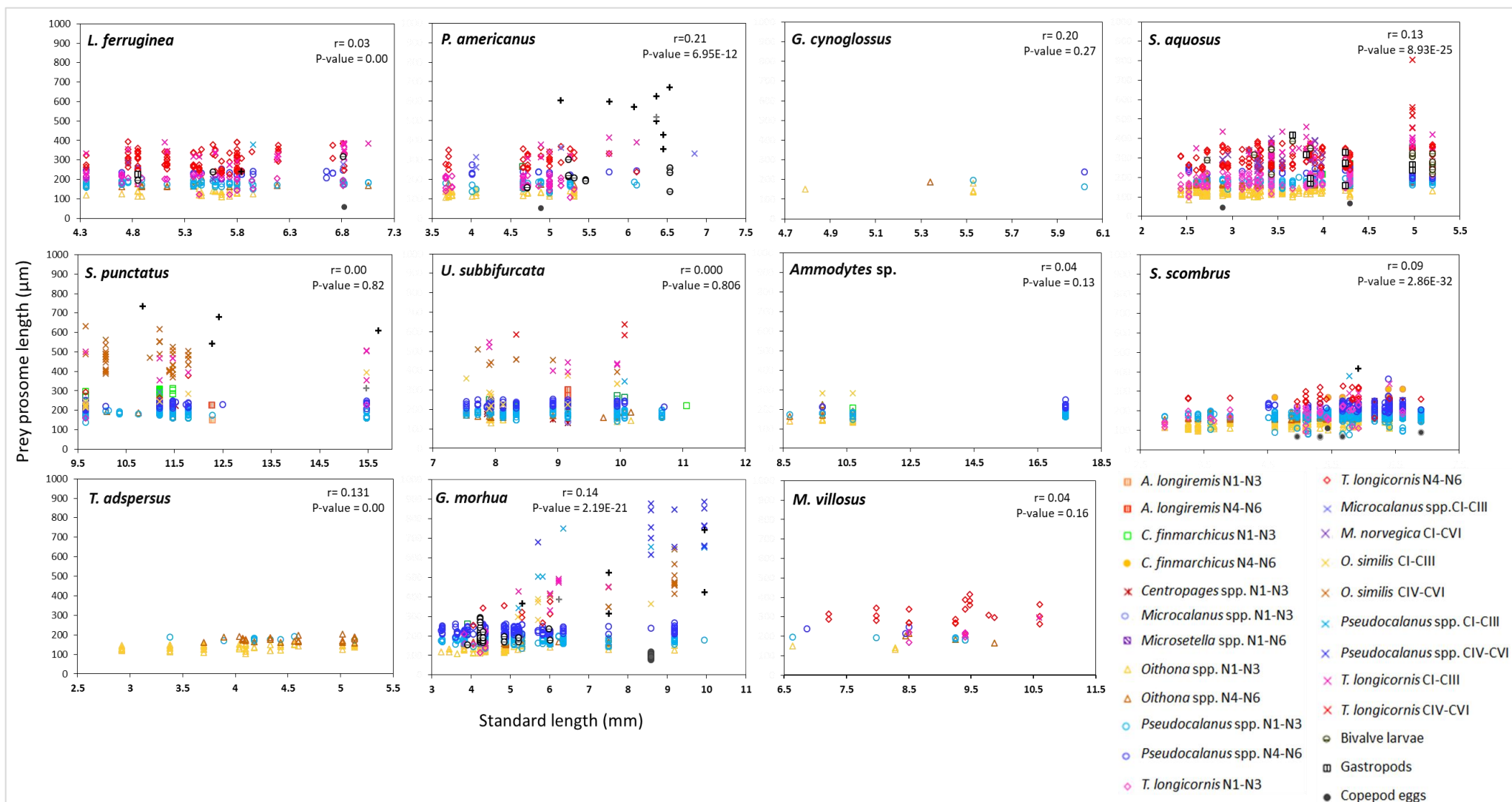
**Fig. 8.** Chesson's alpha ( $\pm$ SE) selectivity index calculated for the most frequently consumed prey taxa in the diet of larval species (Y-axis varies according to size range). Dotted lines indicate the thresholds values for a strong positive and strong negative selection. N: nauplii; developmental stages 1 to 6; C: copepodite; developmental stages I to VI.

Prey size increased with larval size in 6 (*G. morhua*, *L. ferruginea*, *P. americanus*, *S. aquosus*, *S. scombrus* and *T. adspersus*) out of 11 species, showing a significantly positive correlation (Table 4), whereas prey size of the other 5 species (*G. cynoglossus*, *S. punctatus*, *U. subbifurcata*, *Ammodytes* sp. and *M. villosus*) did not increase with larval size (Fig. 9). Although a significant correlation was observed between prey size and larval size in six species, no major shift in diet was observed. Main prey species (in particular nauplii of *Pseudocalanus* sp., *T. longicornis* and *Oithona* sp.) were ingested over the whole larval size range considered, however, in some species larger prey were added to the diet at large larval sizes. The pleuronectiform *S. aquosus* and *L. ferruginea* shifted away from small nauplii of *O. similis* at standard lengths of 5.0 and 5.9 mm, respectively. *S. aquosus* added bigger copepodites stages of *T. longicornis* to its diet during that transition. A similar shift was observed in the pleuronectiform *P. americanus* at about the same size, ingesting larger prey, such as Diplostraca.

**Table 4.** P-value and Pearson correlation coefficient of the relationship between prey size and larval SL. Significant values are shown in bold.

Species	N	p-value	Correlation Coefficient r
<i>L. ferruginea</i>	30	<b>0.002</b>	0.18
<i>P. americanus</i>	26	<b>&lt; 0.001</b>	0.46
<i>G. cynoglossus</i>	5	NS	0.44
<i>S. aquosus</i>	27	<b>&lt; 0.001</b>	0.35
<i>S. punctatus</i>	26	NS	0.02
<i>U. subbifurcata</i>	30	NS	0.01
<i>Ammodytes</i> sp.	5	NS	0.20
<i>S. scombrus</i>	30	<b>&lt; 0.001</b>	0.31
<i>T. adspersus</i>	19	<b>&lt; 0.001</b>	0.36
<i>G. morhua</i>	29	<b>&lt; 0.001</b>	0.37
<i>M. villosus</i>	20	NS	0.21

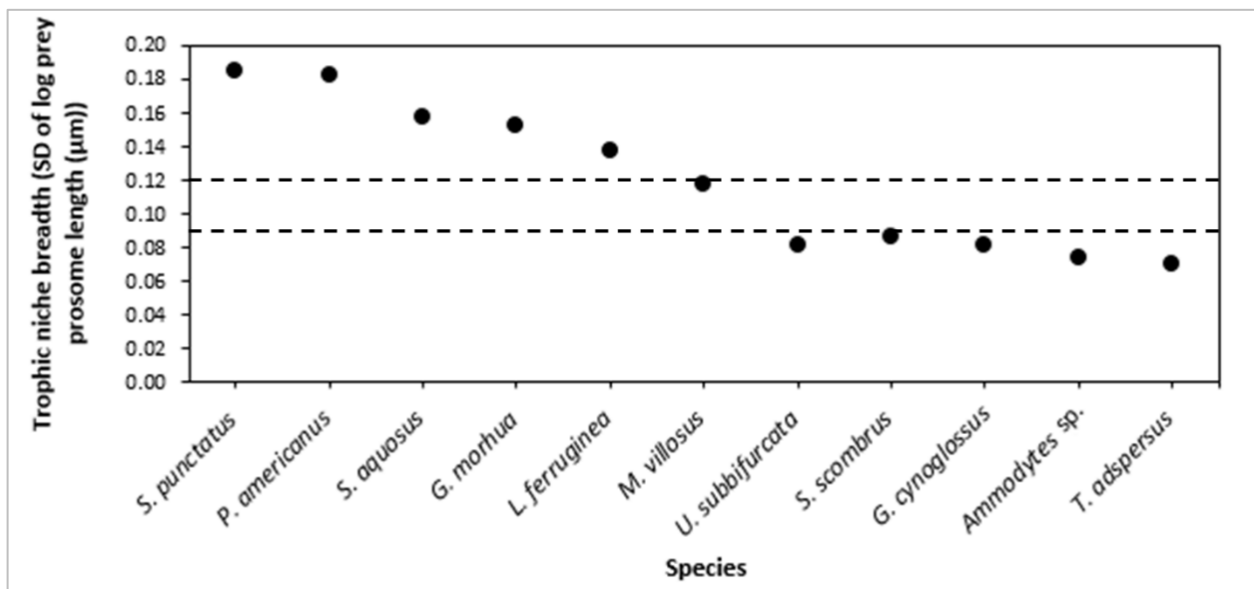
NS: Not statistically significant



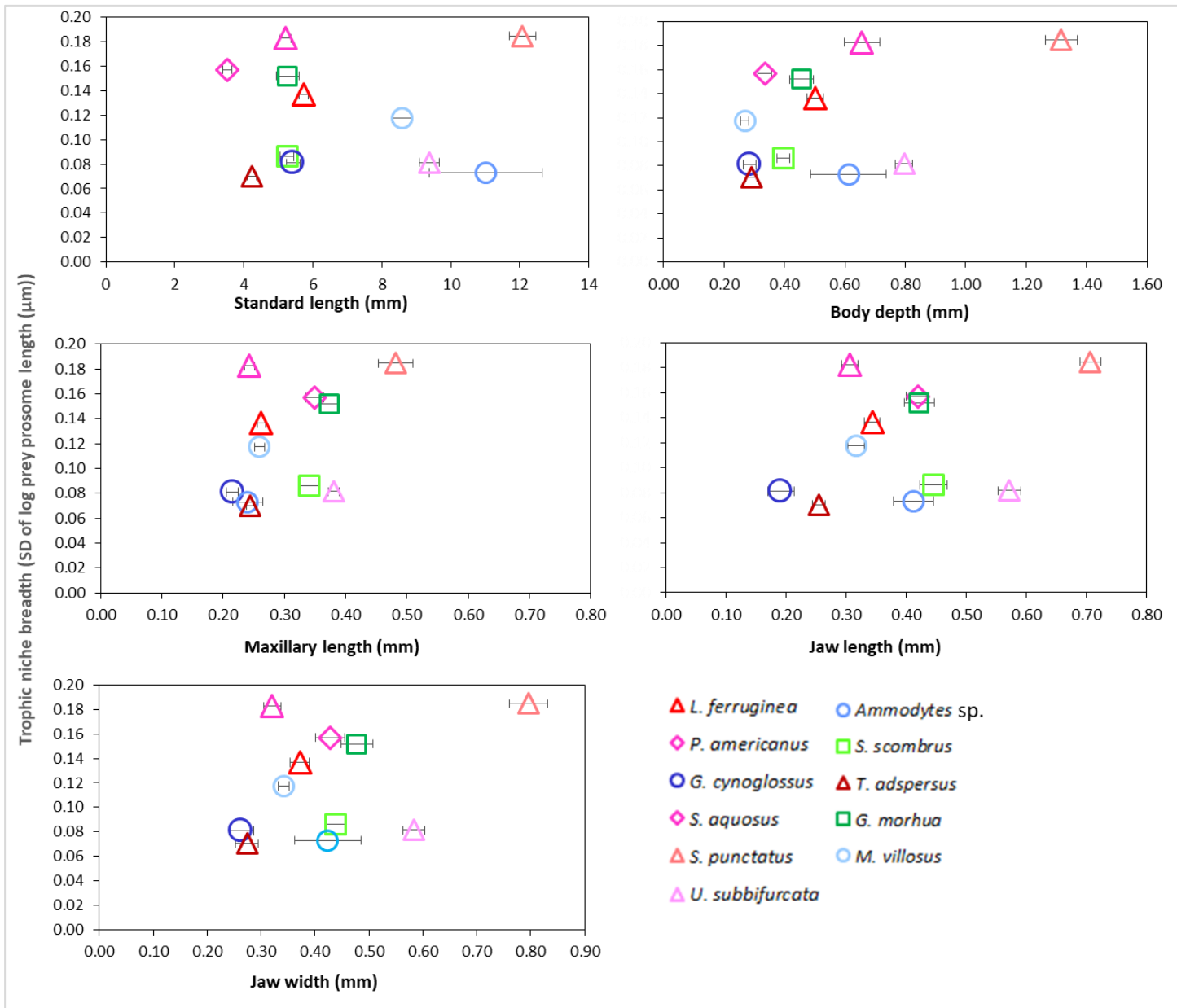
**Fig. 9.** Size and developmental stage of prey consumed as a function of larval SL of each species. All individual prey detected in the stomach of each dissected larva were represented.

#### 2.3.4.1 Niche breadth

Dietary niche breadth differed among species and varied from 0.08 to 0.18 (Fig. 10). Five species were characterized by a narrow niche breadth  $< 0.09$ , while seven species had a wider niche breadth  $> 0.12$ . With the exception of *G. cynoglossus*, pleuronectiform species all ranged within the wide niche breadth group. Perciform species showed the opposite pattern, with all species exhibiting a narrow niche breadth except for *S. punctatus*. The gadiform *G. morhua* and the osmeriform *M. villosus* also displayed a relatively wide niche breadth. No relationship was recorded between trophic niche breadth and morphological characteristics across species (Fig. 11).



**Fig. 10.** Trophic niche breadth, measured as the standard deviation of log-transformed prey size averaged across all larvae of each species. Dotted lines represent thresholds under and above which niche breadth was considered narrow and wide, respectively.



**Fig. 11.** Trophic niche breadth as a function of the morphological characteristics of each species of fish larvae. Each group of morphologically similar species (from the ANOSIM test) was represented by a unique symbol.

## 2.4 DISCUSSION

### 2.4.1 The relationship between morphology and prey selectivity

The larval stage corresponds to the continuation of ontogenic processes initiated in the embryonic stage and the beginning of a period of physiological, anatomical and morphological transformations important for the preparation of fish larvae for the beginning of exotrophic life (Gatesoupe *et al.*, 1999), a known critical period for fish larvae (Houde, 2008). All of these transformations are usually accompanied by an increase in body mass in response to external feeding. Throughout the early ontogeny, particularly during the feeding transition period, feeding success is an essential prerequisite for larval survival and development. Feeding success depends on the development of several morphological structures related to prey search efficiency (standard length and body depth affecting speed), prey capture (the mouth and the two maxillaries), and prey ingestion and digestion (the digestive system). Larval species compared in the present study were morphologically diverse. This morphological disparity reflected major differences in the mouth and its associated organs as well as body shape, including the standard length relative to body depth and the shape of the digestive tract. Our analyses indicated that despite this high morphological diversity, the vast majority of species selected for the mid-sized copepod *Pseudocalanus* sp.. These results are not consistent with those of Sabatés & Saiz (2000), who attributed the high variability in feeding selectivity observed among larval Myctophiform species to interspecific morphological differences that characterize the larvae during their development. Similarly, a synthesis of 204 published studies by Llopiz (2013) reported clear differences in diet among larval taxonomic orders (Clupeiformes, Myctophiformes, Perciformes, Gadiformes, and Pleuronoctiformes) for some prey types of given sizes.

Much of the research dealing with feeding patterns in larval fish (e.g. Shirota, 1970; Hunter, 1981) has shown that larval fish prey selectivity is closely related to mouth size, which dictates the upper limit of prey size (Govoni *et al.*, 1983; Munk, 1992; Sabatés & Saiz 2000; Scharf *et al.*, 2000; Østergaard *et al.*, 2005). For example, Dabrowski & Bardega (1984) indicated that the maximum diameter of food particles ingested by some fish species corresponds to the average



mouth width. Hunter's (1977) study of northern anchovy (*Engraulis mordax*) larvae provides a good example showing a reasonably close correspondence between mouth width and the maximum prey width. In general, however, larval fish prefer prey that are smaller than the maximum size allowed by their mouth gape (Last, 1978a,b; Economou, 1991; Krebs & Turingan, 2003; Yúfera & Darias, 2007). Interestingly, Pepin (2022) reported that larger gape at first feeding was linked to a higher relative proportion of calanoid nauplii in the diet relative to cyclopoid nauplii. These observations provide a potential explanation for the strong selection displayed by fish species in the present study for calanoid copepod nauplii *Pseudocalanus* sp.. In addition, we found that the diet of the two species characterized by the lowest jaw width, *G. cynoglossus* and *T. adspersus*, was heavily dominated by cyclopoid nauplii in terms of numbers compared to calanoid nauplii (Table 2). As cyclopoid nauplii are much smaller than the calanoid nauplii consumed by other species, we infer that jaw length drives to some extent the size-spectrum and composition of prey consumed by larvae. Overall, the relationship between prey size and mouth parameters however remained weak in larval species from the southern Gulf of St. Lawrence.

In a pioneering study on larval fish trophodynamics, Shirota (1970) showed that fish larvae feed on prey items characterized by a mean width corresponding to 20-50% of the maximum gape size. This result was supported by a large body of subsequent research (e.g. Bremigan & Stein 1994; Fernández-Díaz *et al.*, 1994; Busch, 1996; Munk, 1997; Cunha & Planas, 1999; Krebs & Turingan, 2003; Østergaard *et al.*, 2005; Yúfera & Darias, 2007). Moreover, Michaletz *et al.* (1987) found that larvae of different species with similar mouth gape feed on zooplankton of different sizes. These observations of a wide range of prey size in relation to gape size could explain the absence of a clear relationship between prey size and mouth parameters in our study. In addition to prey size, prey shape (the combination of length, width and height) should be considered as a critical dimension for successful feeding given that larval fish generally engulf and swallow their prey whole (Peck *et al.*, 2012). For example, Gliwicz *et al.* (2004) reported that European smelt (*Osmerus eperlanus*) preferred elongated (*Daphnia* spp., *Diaphanosoma* spp.) over compact-bodied (*Bosmina* spp., *Chydorus* spp.) diplostracans.

It is possible that the lack of a clear relationship between mouth characteristics and prey size is in part attributable to an increase in prey diversity in the diet, that is more important than that in prey size, as larvae grow. For example, the rapid rate of increase in mouth size of *P. americanus* has been shown to be associated with its ability to increase prey diversity (Pepin 2022). Furthermore, Deary *et al.* (2017) showed that as elements of the feeding apparatus (i.e., oral and pharyngeal jaw elements) develop, sciaenid larvae add additional prey categories to their diet, which becomes more varied. These observations suggest that in addition to maximum prey size, the level of feeding apparatus development largely determines the extent of the trophic niche.

Body size is also a key determinant of the types, size and number of prey items that can be ingested by the larval fish. Capture and prey-seeking efficiency, and thus feeding success, generally increase with larval length (e.g. Hunter 1980; Yúfera & Darias, 2007). The better hunting skills of larger individuals is partly due to the positive link between somatic growth (size) and feeding apparatus development, but also to the fact that they can swim longer distances than smaller larvae that exhibit limited swimming capacity (Hunt von Herbing & Gallager, 2000). This principle is related to the Reynolds number ( $Re$ ), a dimensionless parameter indicating the ratio of inertial forces to viscous forces in fluids, which increases with body size. Species characterized by smaller larval length are thus likely characterized by slower flow velocities and therefore higher energetic expenditure would be required for swimming. Dietary differences observed between the different larval species in the present study could thus be partly attributable to differences in hunting performance related to size. China & Holzman (2014) suggested that even minute differences in larval size at hatching could result in a dietary advantage at low Reynolds number. Note that marked differences in larval size among species in this study are primarily due to species-specific differences in size at hatching, given that larvae share the same ontogenic stage (i.e. pre-flexion). A positive relationship between average prey size and larval size was reported by several authors (e.g. Govoni *et al.*, 1983; Kellermann, 1990; Young & Davis, 1990; Pepin & Penney, 1997; Sabates & Saiz, 2000) as pointed out in the present study in a number of species such as *G. morhua*, *L. ferruginea*, *P. americanus*, *S. aquosus*, *S. scombrus* and *T. adspersus*. The lack of significant relationships between prey size and standard length in other species (*G. cynoglossus*,

*S. punctatus*, *U. subbifurcata*, *Ammodytes* sp. and *M. villosus*) could be due to the small number of larvae considered in the analysis or to the large number of larvae with little or no prey in the stomach. Taking *L. ferruginea* as an example, the correlation between prey size and larval size was weak ( $r = 0.18$ ) but significant because the larvae analyzed all had full stomachs. Overall, even though morphological traits such as species-specific differences in mouth parameters and body size likely influenced diet composition, the fact that the vast majority of species presenting various shapes and size shared a common main prey lead us to conclude that larval morphological characteristics are not the only factor determining the diet composition of larval fish and that feeding behavior may be the most important driver to consider.

#### **2.4.2 Prey selectivity: Importance of *Pseudocalanus* sp. and *Temora longicornis***

A growing body of literature indicates that for a vast majority of marine fish species, the larval stage does not ingest potential zooplankton prey solely based on their relative abundance in the environment, but instead select for a limited number of zooplankton taxa (Robert *et al.*, 2014). In fact, most larval fish species select for particular species of copepods (see Table V of Robert *et al.*, 2008). Consistent with past investigations, copepod nauplii accounted for the major component of the gut content of all larval fish species during the pre-flexion stage in the present study. The dominance of copepod nauplii in the diets of all species is probably attributable to the combination of a small size and lower ability to detect and avoid attacks from larval fish relative to advanced copepodite stages (Winfield *et al.* 1983). Even though we observed important morphological differences among larval species, the majority of larval fishes consistently showed, independently of their size, a preference for the two medium-sized calanoid copepod nauplii *Pseudocalanus* sp. and *T. longicornis*, whereas the nauplii of the small, but abundant cyclopoid *Oithona* sp. were only selected for by 2 out of 9 species.

According to Sabatés & Saiz, (2000) prey size is one of the main factors involved in the prey selectivity of larval fish. Based on this assumption, we argue that medium-sized copepods have been selected because they fall within the optimal size range that larvae ingest. As fish larvae are

primarily visual feeders (Govoni *et al.*, 1986), their perceptive abilities depend on movement behavior of potential prey, which can elicit a feeding response in larval fish (Wright & O'Brien, 1982; Kiørboe & Visser, 1999). Peterson & Ausubel (1984) determined that the nauplii of *T. longicornis* were strongly selected by mackerel larvae because they are much more mobile and easily visible at a greater distance than other potential prey such as the nauplii of *Acartia hudsonica*. Moreover, *O. similis* generally displays a low level of activity compared to calanoid species, which are often considered to show constant and predictable movements that could be relatively easier to detect by larval fish (Buskey *et al.*, 1993; Heath, 1993; Hwang & Turner, 1995; Paffenhofer *et al.*, 1996). The selectivity towards medium-sized prey might be related to an advantage in energy gain, according to the optimal foraging theory (Schoener, 1971; Werner & Hall, 1974). Based on carbon ingested, we consider nauplii of *Pseudocalanus* sp. as a key prey taxon to support the metabolic requirements for growth and survival of perciform species, while *T. longicornis* nauplii provide the energy for the osmeriform *M. villosus* and pleuronectiform species except for *G. cynoglossus*. Our results contribute to growing evidence that a wide variety of larval fish species have a tight feeding relationship with *T. longicornis* (e.g. Peterson & Ausubel, 1984; Castonguay *et al.*, 2008) and *Pseudocalanus* sp. (e.g. Heath & Lough, 2007; Castonguay *et al.*, 2008; Robert *et al.*, 2009). Similarities in preference for the same taxa among fish species sharing the same habitat might lead to inter- and/or intra-specific competition for food at low prey abundance, but our data did not allow testing this hypothesis.

Some larval species such as *P. americanus* exhibited positive preferences for larger and therefore carbon-rich prey (*Evadne* sp. and bivalve larvae), even though the highest alpha values were still recorded for the mid-sized calanoid copepod *Pseudocalanus* sp.. In theory, the preferred prey is the one that provides the highest net gain of energy and essential nutrients (Schoener, 1971; Werner & Hall, 1974; Pearre, 1986). For this reason, larval fish tend to shift their preferences for larger prey as they grow (Stoecker & Govoni, 1984; Last, 1978a,b; Wainwright & Richard, 1995). In the present study, such a trend was observed for *S. aquosus* and *P. americanus* larvae, which added larger prey items to their diet as they increased in size. The continued inclusion of small prey items in the diets of these predators however contrasts with the conventional hypothesis of optimal foraging, which raises the question: Why would large larvae continue to select for small

prey? The relative abundance of potential prey taxa in the larval feeding environment may affect selectivity. Consequently, larvae may ignore larger prey when smaller prey are at high relative abundance in their feeding environment, which allows them to minimize their food-seeking time and subsequently ensure a high net energy gain (Schoener, 1971; Werner & Hall, 1974). Such a strategy could have driven the diet composition of *S. aquosus* larvae, which was heavily dominated by the most abundant item in the prey field, N1-N3 stages of *Oithona* sp. nauplii (Table 2). To maximize their net energy gain, the limitation in the size of prey ingested by *S. aquosus* larvae was likely compensated by high ingestion rates, reflected by high prey numbers in the guts. Other studies that have examined the size relationships between larvae and their potential prey types have found an increase in the sizes of specific prey types, such as calanoid copepods (Catalán *et al.*, 2007; Simonsen *et al.*, 2006) or larval fish prey of piscivorous larvae (Llopiz & Cowen, 2008), but not in other prey types that larvae continue to include in their diets as they grow. The overall results show that prey selection by larval fish is not only related to prey size, but to several other factors that set restrictions on the types of ingested prey. These being both the size, the shape, the carbon richness and the availability in prey field.

### **2.4.3 Importance of medium-sized copepods for the survival of fish larvae**

The results of the present study showed the importance of the naupliar stages of the calanoid copepod *Pseudocalanus* sp. in the feeding and subsequent survival of a majority of the coexisting fish larvae in the SGS, especially the three perciform species (*U. subbifurcata*, *Ammodytes* sp. and *S. scombrus*) and the gadiform *G. morhua*, for which this key copepod was the most important prey in terms of numbers and carbon. Beyond prey selectivity, the study by Robert *et al.* (2009) revealed a strong relationship between the growth of *S. scombrus* larvae and the abundance of *Pseudocalanus* spp. nauplii. Another study conducted on *S. scombrus* (Castonguay *et al.*, 2008) showed the key role of the availability of the two copepods *Pseudocalanus* sp. and *Temora longicornis* in driving fluctuations in year-class strength. Furthermore, *Pseudocalanus* sp. was identified as a key prey for feeding success of the mid-larval stages of Atlantic herring (*Clupea harengus*) in Newfoundland waters (Wilson *et al.*, 2018), and for the successful recruitment of

capelin (*Mallotus villosus*) in the same area (Murphy *et al.*, 2018). Results from our study have shown that nauplii of *Pseudocalanus* sp. constitute a significant component of the diet of *G. morhua* larvae, especially the early N1-N3 stages, which were strongly selected for. Similarly, Heath & Lough (2007) found a strong dependence of larval cod on *Para/Pseudocalanus* spp. for southern stocks on both sides of the Atlantic. Strong reliance of a species on a specific prey taxon may result in vulnerability to seasonal or interannual changes in zooplankton community structure and abundance (Robert *et al.*, 2009, 2011). The study by Hinrichsen *et al.* (2002) provides a good example, as the highest survival rates of larval Baltic cod *G. morhua* occurred in spring and early summer when the medium-sized copepod *P. elongatus* was available in the larval prey field. In contrast, in the absence of *P. elongatus*, high survival rates were only observed later in the year or if larvae were transported into shallower coastal areas. Möllmann *et al.* (2003) reported that relatively low numbers of *P. elongatus* available in the prey field during spring generally resulted in reduced herring growth. Based on these studies, we infer that variability in the availability of the preferred prey on a seasonal and/or annual time scale could constitute an important driver of recruitment for fish stocks.

Generalist species that feed on a wide range of prey taxa, such as the two pleuronectiforms *P. americanus* and *S. aquosus*, and the perciform *U. subbifurcata*, may show higher potential adapting to spatio-temporal variations in zooplankton prey supply and could be advantaged over specialists when preferred resources are limited. In the case of a depleted food environment, we hypothesize that specialist species may be forced to seek an alternative prey that can meet their metabolic needs for growth and survival. This hypothesis was partly supported by Hinrichsen *et al.* (2002), who showed that even in the absence of *P. elongatus*, late-hatched Baltic cod larvae, a species that shows a strong feeding preference for *Pseudocalanus* sp., were more likely to survive because of increasing abundance of copepod nauplii of other species, primarily the copepodite stages of *T. longicornis* and *Acartia* spp. that accumulate in June to produce next summer generations. Paradis *et al.* (2012) also indicated that when preferred prey such as *Pseudocalanus* spp. were less abundant or absent in the field prey, Atlantic mackerel (*S. scombrus*) larvae switched to an opportunistic generalist feeding behavior by consuming mainly nauplii of

*Oithona* spp. A better understanding of flexibility in feeding strategy for larvae of a given species appears to be of crucial importance to predict potential survival rate. Pepin (2022) suggested that periods characterized by suboptimal feeding conditions might be an ideal timing to carry out such research given that species with greater dietary flexibility (generalists) should then be able to cope more effectively with variations in prey abundance and, therefore, show higher survival relative to specialists.

The majority of ecosystem studies focus on energy transfer by large calanoid copepods such as *Calanus finmarchicus* and *C. hyperboreus* (e.g. Williams *et al.*, 1994). However, our results and that of several previous studies indicate that medium-sized calanoid copepods likely play an important role in recruitment regulation for many species. The importance of medium-sized copepods, and in particular *Pseudocalanus* spp., has been confirmed in other ecosystems. An Ecopath with Ecosim Baltic Proper food–web model (Balt- ProWeb), which was developed by Tomczak *et al.* (2012) to simulate trophic interactions and their flows in the Baltic Proper, showed that the highest energy flows from the pelagic food web directed to sprat (*Sprattus sprattus*) originated from the medium-sized copepods *Temora* 14 t km<sup>-2</sup> and *Pseudocalanus* 11.4 t km<sup>-2</sup>. In comparison, other zooplankton taxa only represented a flux of 7.16 t km<sup>-2</sup>. Given the crucial importance of mid-sized calanoid copepods in various ecosystems, it is important to gain an understanding of factors driving their population dynamics. A model developed by Ji *et al.* (2013) for the Scotian Shelf revealed that *Pseudocalanus* spp. abundance is regulated by a mixture of top-down effects through a trophic cascade involving pelagic fish predators, and bottom-up effects from variability in the biomass and timing of the phytoplankton bloom. A similar exercise in the SGSL could help further understand how environmental variability may affect the recruitment potential of several fish stocks in the region.

## 2.5 CONCLUSION

Our results showed that despite the great morphological diversity that exists among larval species of the SGSL, the majority of species selected for *Pseudocalanus* sp.. This result indicates

that the behavior of larvae and that of their potential prey likely play a more important role than larval morphological characteristics in driving the foraging patterns in these coexisting larval fish species. Our results also suggested that the feeding success and survival of a wide range of marine fishes in the SGSL is largely dependent on a single copepod species among the many taxa that compose the zooplankton assemblage. The abundance of *Pseudocalanus* sp., and the timing of its peak abundance during the season relative to larval emergence, are factors that could be considered to improve stock assessment. Future studies should investigate the drivers of variability in the abundance and phenology of this key copepod, and how these drivers could regulate recruitment strength of SGSL species.



## **CHAPITRE 3 :**

### **CONCLUSION GÉNÉRALE**

Ce mémoire a été réalisé dans le but d'améliorer nos connaissances sur la communauté ichtyoplanctonique du sud du golfe du Saint-Laurent en général et, en particulier des eaux du plateau madelinien, un système dominé par les petits copépodes cyclopoïdes (*Oithona similis*) et les copépodes calanoïdes de taille moyenne, principalement représentés par *Pseudocalanus* sp. et *Temora longicornis*. Cette productivité zooplanctonique fait du plateau madelinien une zone propice au développement rapide du stade larvaire de nombreuses espèces de poissons (de Lafontaine *et al.*, 1991; White & Johns, 1997). Le présent projet de recherche représente une étude comparative de la composition et de la taille des proies consommées par les stades larvaires de 11 espèces de poissons capturées simultanément sur une seule journée. Malgré que l'échantillonnage soit limité à une courte période de collecte, une étude comparative comprenant un grand nombre d'espèces échantillonnées simultanément revêt un intérêt particulier car la majorité des études comparatives réalisées à date (par exemple Shirota, 1970; Pearre, 1986) font face à des biais potentiels en lien avec des différences dans le moment de l'échantillonnage selon l'espèce, ce qui implique des différences dans les conditions environnementales pouvant influencer notre perception de la sélectivité des larves. Dans mon étude, nous avons testé l'hypothèse que les larves des différentes espèces de poissons présentes au même moment dans le plancton s'alimentent de proies différentes en fonction de différences dans leur morphologie. Ainsi, mon projet de recherche visait à améliorer nos connaissances de l'importance des caractéristiques morphologiques pour déterminer le succès d'alimentation et le potentiel de survie à un stade critique du cycle de vie des poissons.

Néanmoins, les résultats obtenus indiquent que malgré la grande diversité morphologique qui caractérise les 11 espèces de larves de poissons de la présente étude, la plupart de ces espèces a montré une préférence pour les nauplii du copépode calanoïde *Pseudocalanus* sp.. Ces résultats suggèrent que la sélectivité des proies est le résultat d'un processus influencé par l'interaction d'un

certain nombre de facteurs entrant en jeu lors de l'interaction prédateur-proie; ceux-ci étant potentiellement des facteurs morphologiques (Last, 1980; Sabatés & Saiz, 2000; Østergaard *et al.*, 2005), physiologiques liés à la perception et la capacité d'attaque (Browman & O'Brien, 1992a,b), comportementaux (Hunter, 1980; Peterson & Ausubel, 1984; Munk 1992, 1995; Shoji & Tanaka, 2006), et environnementaux (Cushing, 1990; Fox *et al.*, 1999). Aucun facteur unique ne peut déterminer à lui seul le régime alimentaire, ainsi que la capacité de la larve à se nourrir efficacement des différentes composantes de la communauté zooplanctonique. Nos résultats renforcent également l'importance marquée du copépode *Pseudocalanus* sp. pour l'alimentation, et par conséquent la croissance, le développement et la survie des larves de plusieurs espèces de poissons du SGSL. Cependant, la préférence des espèces larvaires pour un même taxon est susceptible d'augmenter le risque de compétition inter- et intra-spécifique pour la ressource alimentaire. Pour savoir si la nourriture est suffisamment abondante pour éviter la compétition alimentaire, il sera alors important de mener des études futures visant à (i) évaluer le nombre de copépodes disponibles par larve en calculant la densité des larves présentes dans un site donné et la comparer avec celle de la communauté zooplanctonique et (ii) déterminer le taux d'ingestion des larves. Sur la base de l'efficacité de digestion et d'assimilation des proies, il sera également utile de quantifier l'énergie nécessaire pour couvrir les coûts métaboliques de la larve de poisson, ce qui permettrait l'estimation de la quantité de proies qui doit être ingérée par unité de temps pour permettre une croissance et un développement adéquats.

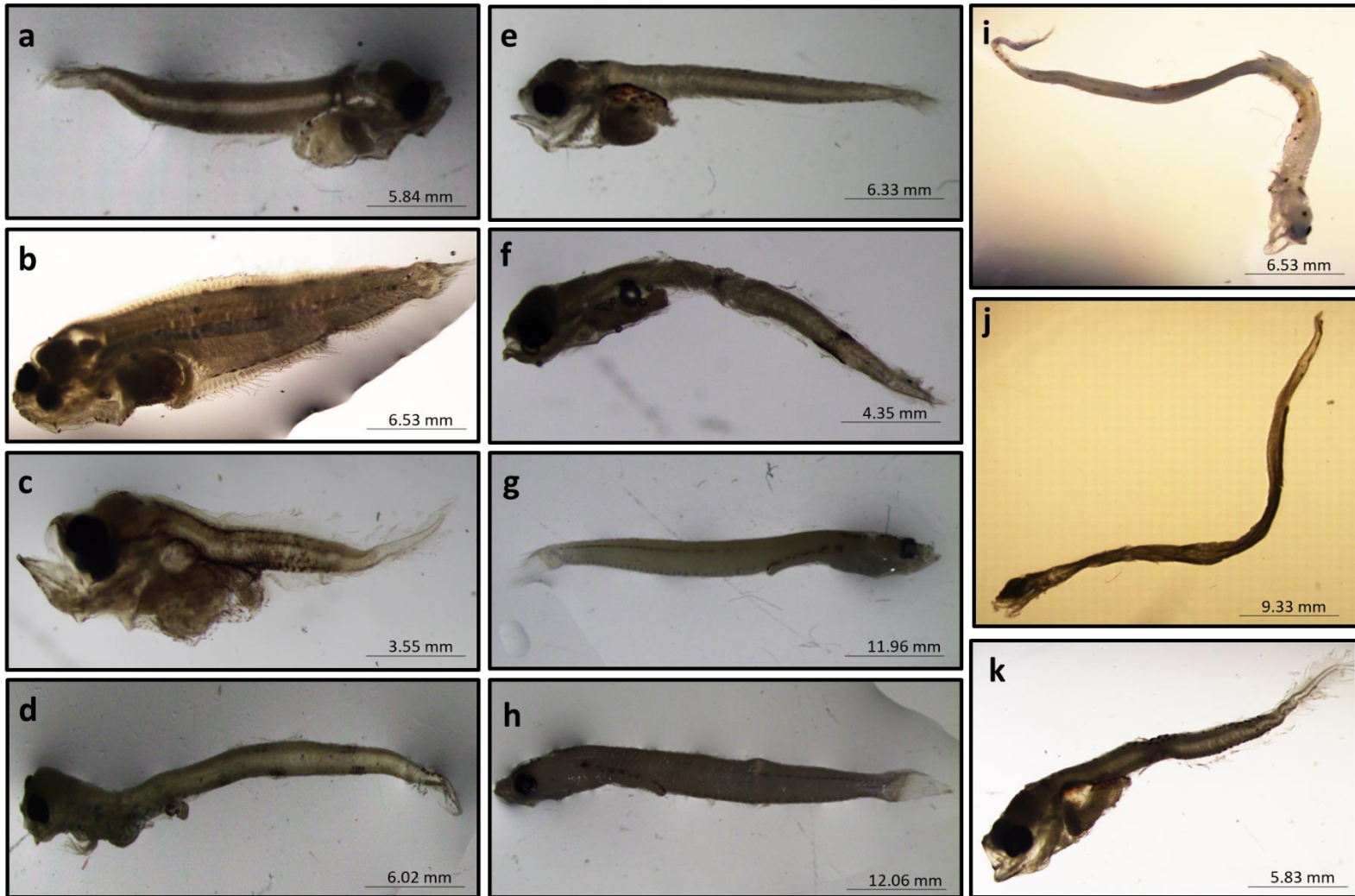
La collection unique de larves à la base de la présente étude a offert l'opportunité de comparer le régime alimentaire du stade larvaire de 11 espèces de poissons (4 ordres et 8 familles) capturées simultanément. Cette collection historique a été assemblée en 1998, une période caractérisée par une haute diversité larvaire dans le SGSL. Cependant, au cours des 20 dernières années, le GSL a reconnu une chute drastique de l'abondance de nombreuses espèces de poissons. C'est notamment le cas de la morue franche (*Gadus morhua*), de la plie canadienne (*Hippoglossoides platessoides*), de la limande à queue jaune (*Limanda ferruginea*) et du maquereau bleu (*Scomber scombrus*). Ceci nous oriente à se questionner quant aux conséquences de ces changements au niveau de la communauté ichtyoplanctonique. Conformément à la théorie

du forçage descendant (contrôle top-down) du GSL et suite au relâchement de la pression de prédation, la diminution des principaux prédateurs (les larves de poissons) serait-elle suivie d'une augmentation de l'abondance de leurs proies (zooplanctons) ? Cette augmentation inclurait-elle les copépodes de tailles moyennes, notamment le calanoïde *Pseudocalanus* sp. qui a été fortement sélectionné par les larves étudiées ici? Le rapport scientifique réalisé par Blais *et al.* (2021) a révélé que la biomasse zooplanctonique était généralement inférieure à la normale dans le SGSL suite à la diminution d'abondance des grands copépodes calanoïdes comme par exemple *Calanus hyperboreus*, mais l'abondance de *Pseudocalanus* sp. a récemment augmenté. Cette augmentation de *Pseudocalanus* sp. pourrait être due à un forçage ascendant (contrôle bottom-up) résultant de changements observés dans la composition de l'assemblage phytoplanctonique au cours des dernières années (Blais *et al.*, 2021).

Il est important de prendre en compte les limites de la présente étude. Puisque les larves de poissons des trois stations ont été capturées au cours de la même journée, il n'a pas été possible de (i) comparer la sélectivité alimentaire sur la base des variations interannuelles de la communauté zooplanctonique du milieu d'échantillonnage, (ii) étudier la variabilité dans le régime alimentaire en fonction des changements morphologiques que les larves subissent au cours de leur développement ontogénique et (iii) quantifier l'influence de la morphologie sur la croissance larvaire. Il s'avère donc important d'axer les futurs travaux sur la variabilité ontogénique et interannuelle dans la composition du régime alimentaire. Un premier examen pourrait être effectué à partir de la base de données GLOBEC (1997-2000) complète. Puis, pour vérifier l'effet des changements récents de l'écosystème sur le régime alimentaire des larves, un échantillonnage contemporain serait important à considérer. Cet échantillonnage permettrait également de quantifier les changements dans l'abondance relative des stades larvaires de poissons du SGSL. Parallèlement aux études ichtyoplanctoniques comparatives, il serait également important de développer un programme de suivi environnemental visant à identifier les conditions responsables des fluctuations saisonnières et/ou interannuelles dans l'abondance des copépodes d'importance cruciale pour la survie et le développement des larves de poissons, notamment *Pseudocalanus* sp..



## **ANNEXES**



**Fig. AI.** Representation of the 11 species of larval fish in this study. (a) *Limanda ferruginea*, (b) *Pseudopleuronectes americanus*, (c) *Scophthalmus aquosus*, (d) *Glyptocephalus cynoglossus*, (e) *Scomber scombrus*, (f) *Tautogolabrus adspersus*, (g) *Stichaeus punctatus*, (h) *Ulvaria subbifurcata*, (i) *Ammodytes* sp., (j) *Mallotus villosus* and (k) *Gadus morhua*. The value in the lower right corner of each panel represents the standard length of the larva in mm.

**Table AII:** Summary of references on relationships between carbon content (*C*, in  $\mu\text{g}$ ), prosome or total length (*L*, in  $\mu\text{m}$ ), volume (*V*, in  $\mu\text{L}$ ), ash-free dry weight (ADW in  $\mu\text{g}$ ) and dry weight (DW, in  $\mu\text{g}$ ) for the main prey of larval fish

Taxon		Equations	References
<b>Copepods</b>			
<b>Nauplii</b>			
<i>Acartia</i> spp.	C	$3.18 \times 10^{-9} \times \text{PL}^{3.31}$	Berggreen <i>et al.</i> (1988), Fig. 3
<i>Calanus finmarchicus</i>	C	$4.29 \times 10^{-6} \times \text{L}^{2.05}$	Hygum <i>et al.</i> (2000)
<i>Centropages</i> spp.	ADW	$10^{2.2357} \times \log \text{L} - 5.5458$	Klein Breteler <i>et al.</i> (1982)
	DW	ADW + 7 %	Bâmstedt (1986)
	C	44.7 % DW	Mauchline (1998)
<i>Oithona</i> spp.	C	$5.545 \times 10^{-8} \times \text{PL}^{2.71}$	Sabatini and Kiørboe (1994), Fig. 1
<i>Microcalanus</i> spp.	C	$(10^{2.515} \times (\log \text{L}/1000) + 0.975) \times 0.447$	Lee <i>et al.</i> (2003), Fig. 3, (1)
<i>Microsetella</i> spp.	C	$(10^{2.515} \times (\log \text{L}/1000) + 0.975) \times 0.447$	Lee <i>et al.</i> (2003), Fig. 3, (1)
<i>Pseudocalanus</i> spp.	C	$(10^{2.515} \times (\log \text{L}/1000) + 0.975) \times 0.447$	Lee <i>et al.</i> (2003), Fig. 3, (1)
<i>Temora longicornis</i>	ADW	$10^{2.1674} \log \text{L} - 5.5336$	Klein Breteler <i>et al.</i> (1982)
	DW	ADW + 7 %	Bâmstedt (1986)
	C	44.7 % DW	Mauchline (1998)
Unidentified copepod nauplii	C	$(10^{2.515} \times \log (\text{L}/1000) + 0.975) \times 0.447$	Lee <i>et al.</i> (2003), Fig. 3, (1)
<b>Copepodites</b>			
<i>Microsetella norvegica</i>	C	$e^{1.15 \times \ln \text{L} - 7.79}$	Satapoomin (1999)
<i>Microcalanus</i> spp.	C	$10^{3.07} \times \log \text{PL} - 8.37$	Uye (1982)
<i>Oithona similis</i>	C	$9.4676 \times 10^{-7} \text{PL}^{2.16}$	Sabatini and Kiørboe (1994), Fig. 1
<i>Pseudocalanus</i> spp.	C	$(10^{2.85} \times \log \text{PL} - 7.62) \times 0.447$	Liu and Hopcroft (2008), Fig. 1, (1)
<i>Temora longicornis</i>	DW	$10^{2.815} \times \log \text{PL} - 7.181$	Hay <i>et al.</i> (1991)
	C	44.7 % DW	Mauchline (1998)
Eggs	C	$0.14 \times 10^{-6} \times (4/3 \pi (\text{L}/2)^3)$	Kiørboe, 1985
<b>7 copepod species</b> ( <i>C. finmarchicus</i> , <i>C. hyperboreus</i> , <i>T. longicornis</i> , <i>A. longiremis</i> , <i>A.</i> <i>tonsa</i> , <i>C. hamatus</i> and <i>Pseudocalanus</i> spp.)			
Diplostracans	C	$10^{4.15} \times \log \text{L} - 11.15$	Uye (1982)
Gastropods	DW	$6.07 (\text{L} \times 10^{-6})^{2.59} \times 108$	Legendre and Michaud (1998)
	C	22.1 % DW	Omori (1969)
Bivalve larvae	C	$3.06 \times 10^{-8} \times \text{L}^{2.88}$	Fotel <i>et al.</i> (1999), Sect. 3.4
Fish larvae	DW	$10^{4.09} \times \log (\text{L}/1000) - 1.114$	Laurence (1979)
	C	40 % DW	Legendre and Michaud (1998)

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**Table AIII: Densities of frequently consumed prey taxa at each station**

Taxon	Station A	Station B	Station C
Copepods			
Nauplii			
<i>Acartia</i> sp. N1-N3	102.76		0.00
<i>Acartia</i> sp. N4-N6	102.76	85.32	224.25
<i>C. finmarchicus</i> N1-N3	132.13		96.11
<i>C. finmarchicus</i> N4-N6			32.04
<i>Centropages</i> sp. N1-N3	161.49	106.65	96.11
<i>Microcalanus</i> sp. N1-N6	601.91	170.63	32.04
<i>Microsetella</i> sp. N1-N6	1658.92	1535.70	1441.58
<i>Oithona</i> sp. N1-N3	11421.58	13650.63	19124.97
<i>Oithona</i> sp. N4-N6	5314.41	7891.77	5285.80
<i>Pseudocalanus</i> sp. N1-N3	3259.11	4521.77	4661.11
<i>Pseudocalanus</i> sp. N4-N6	968.93	767.85	384.42
<i>T. longicornis</i> N1-N3	3317.84	3327.34	4132.53
<i>T. longicornis</i> N4-N6	3171.03	2858.10	5478.01
Copepodites			
<i>Microcalanus</i> sp. CI-CVI	14.68		0.00
<i>M. norvegica</i> CI-CVI	2613.16	3860.57	5061.55
<i>Oithona similis</i> CI-CIII	1042.33	1578.35	1249.37
<i>Oithona similis</i> CIV-CVI	1893.81	1983.61	2434.67
<i>Pseudocalanus</i> sp. CI-CIII	557.87	447.91	288.32
<i>Pseudocalanus</i> sp. CIII-CVI	367.02	575.89	864.95
<i>T. longicornis</i> CI-CIII	2348.91	2111.58	2819.09
<i>T. longicornis</i> CIV-CVI	499.14	917.15	1089.19
Eggs (<135 µm)	5431.86	4863.04	6198.80
Diplostracans			
<i>Evadne</i> sp.	1409.35	4735.06	2210.42
<i>Podon</i> sp.	264.25	234.62	256.28
Gasteropoda	220.21	618.54	256.28
Bivalve larvae	11333.50	24784.43	18932.76
fish larva			32.04

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